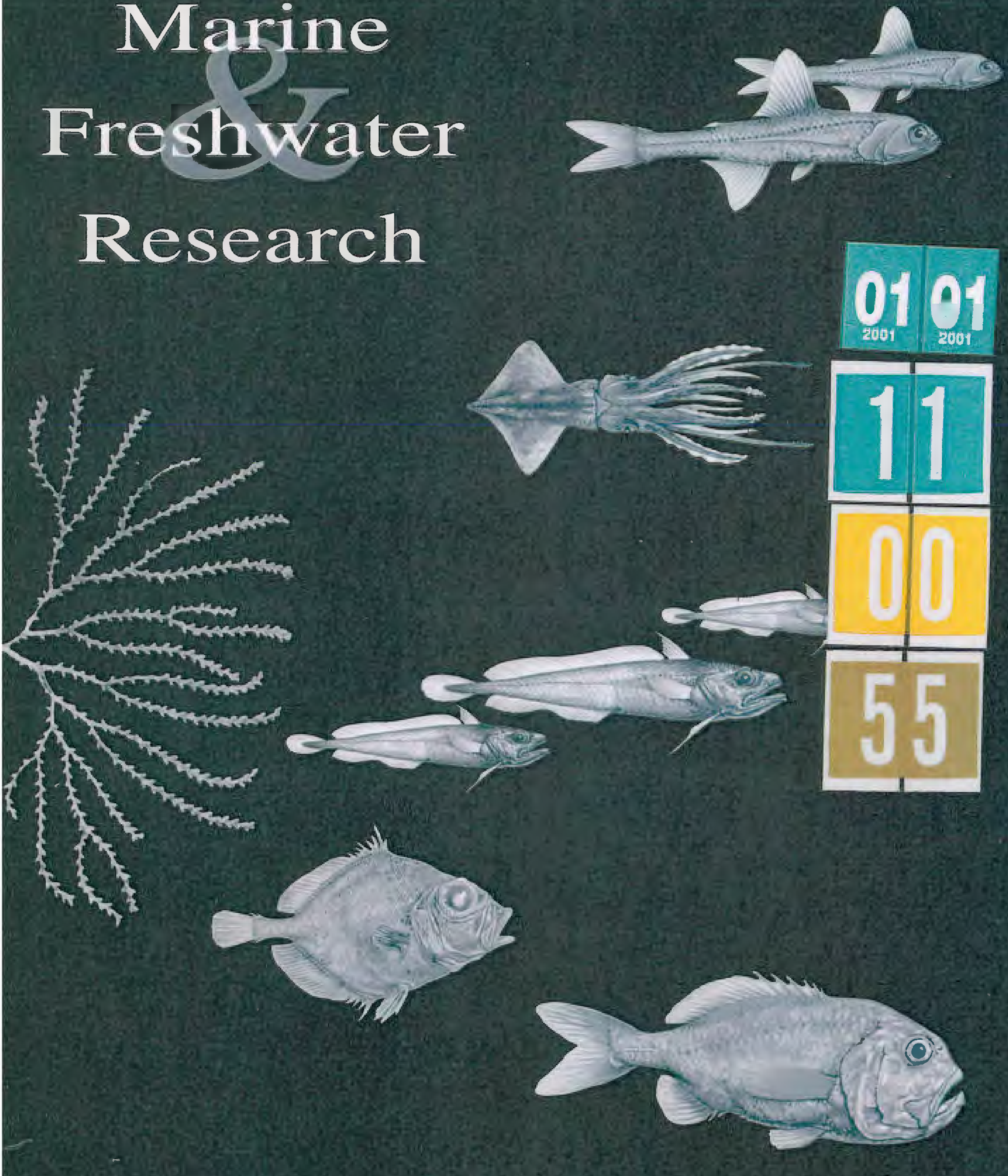
Marine & Freshwater Research



Volume 52(4) 2001

Special Issue: A Complex Quota-managed Fishery: Science and Management in Australia's South East Fishery

Marine and Freshwater Research

An international journal for the publication of original contributions in marine, estuarine or freshwater research.
Papers from the Southern Hemisphere are particularly encouraged, although not to the exclusion of those from the Northern Hemisphere.
This Journal is one of the Australian Journals of Scientific Research published by CSIRO PUBLISHING for the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Australian Academy of Science. Editorial policy for the series is developed by a Board of Standards appointed jointly by CSIRO and the Academy.
CSIRO PUBLISHING requires all authors of a multi-authored paper to agree to its submission. The publisher has used its best endeavours to ensure that work published is that of the named authors except where acknowledged and, through its reviewing procedures, that any published results and conclusions are consistent with the primary data. It takes no responsibility for fraud or inaccuracy on the part of the contributors.

Advisory Committee

Acceptance of papers is the responsibility of the Editor in consultation with the Advisory Committee on behalf of the Board of Standards. All papers are peer reviewed. Committee members may advise the Editor on the selection of referees and may adjudicate in the case of conflicting or adverse reports.

Subscriptions for 2001

Australia and New Zealand
Institutions: Print $A625. Electronic $A625. Print+electronic $A695
Personal rate: Print $A150. Electronic $A135. Print+electronic $A165

Other countries
Institutions: Print $US550. Electronic $US550. Print+electronic $US650
Personal rate: Print $US150. Electronic $US135. Print+electronic $US165
Subscribers outside Australia receive their journals by air mail.

Back issues $75

ISSN 1323–1650

Issued eight times a year

The Instructions to Authors are published in the first issue of each volume. Copies are available on request. Information about the journal, including the Instructions to Authors, is available on World Wide Web at URL

http://www.publish.csiro.au/journals/mfr

Manuscripts and editorial enquiries should be addressed to:

The Editor
CSIRO PUBLISHING
Marine and Freshwater Research
PO Box 1139
Collingwood, Vic. 3066, Australia
(Street address: 150 Oxford Street, Collingwood)
Facsimile: +61 3 9662 7611
email: ann.grant@publish.csiro.au

Subscription enquiries should be addressed to:

CSIRO PUBLISHING
PO Box 1139 (150 Oxford Street)
Collingwood, Vic. 3066, Australia
Telephone: +61 3 9662 7686
Facsimile: +61 3 9662 7555
email: sales@publish.csiro.au

CSIRO

Academy of Science

Marine and Freshwater Research

Contents **Volume 52** **Number 4** **2001**

A complex quota-managed fishery: science and management in Australia's South East Fishery

The fishery and its management

The South East Fishery ecosystem

(continued)

Biology and life history parameters

Quantitative stock assessment

Mar. Freshwater Res., 2001, **52**, 353–59

A complex quota-managed fishery: science and management in Australia's South-east Fishery. Introduction and Overview

Anthony D. M. Smith[A] *and David C. Smith*[B]

[A]CSIRO Division of Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia
[B]Marine and Freshwater Resources Institute, Department of Natural Resources and Environment, PO Box 114, Queenscliff, Vic. 3225, Australia

Why a South-east Fishery Special Issue?

Fisheries science and management is under increasing scrutiny. There are widely held views that fisheries management has been unsuccessful and there is concern for the status of fish stocks worldwide (Mace 1997). There is also increasing community concern regarding the impact of fishing on the ecosystem, particularly by-catch and effects on threatened species. Concurrently there is a move towards participatory or co-management in which stakeholders, particularly industry, are involved directly in the management process (Jentoft 1989). Fishery science is also changing, from prescriptive to descriptive advice, and with increasing recognition of the limitations of single-species approaches and the need for a greater understanding of ecosystem interactions (Pajak 2000).

In Australia, the partnership approach of the Australian Fisheries Management Authority (AFMA) (Smith *et al.* 1999) and management arrangements in most States, such as Victoria's Fisheries Co-management Council, have developed effective mechanisms for collaborative management. The public concern about the impacts of fishing on the ecosystem is reflected in recent changes by Environment Australia to regulations governing fisheries. The most significant change is the requirement to demonstrate ecological sustainability to gain certification for export of all commercial fish species. Australia's fisheries jurisdictions have also recently instituted a practical framework for adopting Ecologically Sustainable Development (ESD). Setting sustainable levels of fishing has, of course, been central to fisheries management and science for a long time, but the focus now is far broader than the target species. Within Australia, these major shifts in focus and their implementation have taken place in a relatively short time.

So why a Special Issue about the South-east Fishery (SEF)? Within the policy framework described above, the fishery provides a striking example of changes in management philosophy and process, and in scientific approach and emphasis. It is also extraordinarily complex. As this issue shows, it has evolved from a simple trawl fishery, operating in a relatively small area, targeting only a few species, to what could be facetiously called a multi-everything fishery. It is a multi-species, multi-fleet/gear fishery that operates across a broad geographical region around Australia's south-east coast including Tasmania, in depths from 30 m to 1200 m. It exploits many species with widely varying life histories and ecologies in numerous habitats. For primarily historical reasons, it has two sectors, each with its own industry association and management advisory committee (MAC). Research and monitoring are conducted by several federal and State agencies. Current management is primarily through ITQs on the major species, but some input controls including area management are also in place. The fishery is managed by a federal statutory authority – AFMA.

Papers in this issue cover a broad range of themes and issues including fishery history, resource assessment, biology, habitats, food webs, the perspectives of the industry, quota trading and management. This contrasts with a previous review of the fishery (Tilzey 1994), in which there is little or no mention of ecosystem issues and for which few quantitative assessments were available. The papers have been organized into four broad groupings, although several could fit into more than one: the fishery and its management; the South-east Fishery ecosystem; biology and life history parameters; and quantitative stock assessments.

Below, we briefly summarize some of the key aspects of these 'chapters' and then identify some issues for the future.

The fishery and its management

The history of the fishery is characterized by three broad overlapping phases (Table 1) although the most dramatic changes have occurred within the past 15 years. These phases encompass developments in the fishery, its management and the science and the processes under which the science is undertaken. The first phase covers the years up to the early 1970s when the fishery operated mostly on the continental shelf off New South Wales and north-eastern Victoria. The fishery was primarily an open-access fishery with no formal processes to coordinate research and monitoring. During the 1970s and 1980s, the fishery

10.1071/MF01029 1323-1650/01/040353

expanded spatially and into upper- and mid-slope waters. Limited entry was introduced and there was coordination of research. In addition, during the end of the period, arrangements to formally involve industry in research commenced. The most recent phase occurred during the 1990s, with the introduction of ITQs, the establishment of an inclusive assessment process and increased interest in fishery–ecosystem interactions.

Tilzey and Rowling (2001) provide a detailed review of the history of the fishery from a scientist's perspective. They refer to the three phases mentioned above as the steam trawl and Danish Seine era, the 'new development' era, and the modern, 'stock assessment' era. The years encompassing these are generally the same as in Table 1. Dealing with the 1980s onwards, Grieve and Richardson (2001), in an interesting comparison with Tilzey and Rowling, describe the recent history of the fishery from a manager's perspective. They discuss whether AFMA has met its fishery management objectives and develop simple indicators of change against which performance can be measured, particularly economic efficiency. Connor and Alden (2001) extend the economic discussion through an analysis of quota markets in the SEF. They conclude that the market is working relatively well and that there is little evidence of ownership concentration (a common criticism of ITQs). There has, however, been little reduction in fishing capacity.

The remaining three papers in this section deal with operational aspects of the fishery. Klaer (2001) presents the first rigorous examination of steam-trawler logbook data for the early years of the fishery (1918–57). This analysis provides an important 'baseline' on the fish assemblages exploited during that period, to which later information can be compared.

Jeremy Prince, who has been a scientific consultant to the trawl industry since 1992, has argued for a number of years that analysis of trends in commercial catch rates must take into account changes in fishing practices due to the introduction of quotas in the fishery. These changes include a shift from targeting individual species to diversifying catch composition in response to quota holdings and market value. Baelde (2001) demonstrates the importance of these changes through a synthesis of fishers' own descriptions of fishing gear and practices.

The development of the fishery in recent years is recorded by Larcombe *et al.* (2001), who describe the spatial distribution and intensity of the current trawl fishery; they find that although effort has increased in recent years, the area fished has actually stabilized and the fishing grounds make up only a small proportion of the total *management* area.

The South-east Fishery ecosystem

The number of papers under this broad heading demonstrates an increased scientific interest in fishery–ecosystem interactions in recent years. Many of the papers derive from a 5-year study of the south-eastern Australian continental shelf (Bax and Williams 2001). This is one of

Table 1. Broad evolutionary phases of the South-east Fishery

	Pre 1970	1970 s, 1980 s	1990 s	The Future
Fishery	Primarily steam trawls and Danish seines operating on continental shelf in eastern zone	Diesel trawlers – expansion to upper and mid slope and into southern and western zones. Development of the non-trawl fishery (gill-net, trap, line)	Some reduction in number of vessels but increase in bottom time	Increasing use of environmentally 'friendly' fishing methods. Better utilization of catch
Management	Mostly open access. Separate State regulation of mesh sizes and minimum legal lengths	Trawl fishery brought under federal jurisdiction and unitized in the mid 1980 s	Non trawl brought under federal management. Introduction of ITQs for 16 species. Development of fishery management plans.	Integration of trawl and non-trawl fisheries. Development of environmental management plan
Research and monitoring	*Ad hoc*	Major programmes initiated by States and Commonwealth agencies. Co-ordination through Demersal and Pelagic Fisheries Research Group (scientists only)	Integrated fishery-wide sampling (CAF[a] and ISMP[b]). Co-ordination through South-east Fishery Assessment Group (all stakeholders)	Increasing direct involvement of industry in research and monitoring
Fishery assessment	No formal stock assessment	Several quantitative stock assessments by scientists. Presentation by scientists to industry and managers	Many quantitative stock assessments and some agreed harvest strategies. Clearly defined stock assessment process with all stakeholders involved	Extension to include broad set of ESD[c] indicators and assessment of ecological impacts of fishing

a. CAF Central Ageing Facility
b. ISMP Integrated Scientific Monitoring Program
c. ESD Ecologically Sustainable Development

only a few integrated studies of the SEF ecosystem. The other major study was undertaken during the 1980s on the Tasmanian upper slope (Blaber and Bulman 1987; May and Blaber 1989). In addition, research on orange roughy in the early 1990s included aspects of the ecology of the mid slope and sea mounts where this species is found (Koslow *et al.* 1994; Koslow 1997; Koslow *et al.* 1997).

The first paper in this section is a review of the literature, integrated with fishers' own views of the SEF ecosystem. In this paper, Prince (2001) argues that the importance of oceanic primary production has been underestimated and that many of the important commercial species forage pelagically. Thus they are not as closely linked to benthic habitats as was previously assumed.

Bax *et al.* (2001) find that the source of primary production on the eastern Bass Strait shelf is oceanic, and that phytoplankton blooms do not contribute directly to sediment organic matter. The importance of eddies to production in the SEF ecosystem is demonstrated by Young *et al.* (2001).

The next two papers in this section deal directly with seabed habitat. Kloser *et al.* (2001) describe a method that uses multi-frequency acoustics with associated 'ground truthing' (benthic samples, sediments, photography and videorecording) to identify seabed structure. Using this information, Bax and Williams (2001) develop a hierarchical approach to mapping seabed habitat as one of the first steps to building a framework of knowledge upon which future spatial management can be based, particularly the management of fishing effort.

Williams and Bax (2001) analyse the spatial structure and composition of the fish communities of the eastern Bass Strait shelf, finding that communities are correlated with depth, latitude and seabed type. They produce a biophysical map by overlaying community patterns on seabed type in the area studied. They discuss their approach in the context of regional marine planning and ecosystem-based management.

Bulman *et al.* (2001) identify 10 trophic guilds through an analysis of >8000 stomach samples from 102 fish species caught on the south-eastern Australian shelf. Importantly, they find that although benthic prey items dominate diets, pelagic prey are important in a subset of commercially and ecologically important species including 12 quota species. They conclude that pelagic production contributes significantly to the SEF.

The final paper in this section describes the effects of fishing on sharks and rays off the New South Wales coast. Graham *et al.* (2001) find that the overall abundance of these species declined to 20% over a twenty-year period. Their results indicate that the biomasses of most species of sharks and rays on the NSW slope declined rapidly as the SEF developed and are now at low levels. They attribute this to the susceptibility of chondrichthyans to fishing pressure, and to the lack of direct management for these species in the SEF.

Overall, the papers in this section reflect a growing understanding of the SEF ecosystem emphasizing temporal variability, spatial complexity, and important links between benthic and pelagic production. This further reinforces the views of fishers, described in Prince (2001). This understanding has potentially important implications for assessment and management.

Biology and life-history parameters

Despite the longevity of the fishery, there is still much that is not known about the biology and life-history parameters of many of the key species, let alone by-product and by-catch species. Papers in this section cover a wide range of studies from genetic population structure to age and growth.

Knowledge of the stock structure of exploited species is a key requirement for effective management. Ward and Elliott (2001) review allozyme, mitochondrial DNA and micro-satellite data for 20 species in south-eastern Australia. For most fish species, there is little genetically detectable population structure. Gemfish is a striking exception. Most fish species show significant differences between Australia and New Zealand but the degree of this difference is generally small. Consequently, most quota species in the SEF are currently managed as one stock, apart from gemfish (two stocks) and orange roughy (which is managed as five stocks, although not on the basis of genetic evidence). However, genetic studies often provide ambiguous results on stock structure, and other information for some species suggests that sub-fishery spatial units may be more appropriate.

Knuckey and Sivakumaran (2001) describe the reproductive characteristics of blue warehou, extending their results in an eggs-per-recuit analysis. Jordan (2001*a*) presents the reproductive biology and early life history of sand flathead. Prince and Griffin (2001) describe the oceanographic factors that influence the timing and location of pre-spawning aggregations of eastern gemfish; this has led to an interesting exchange of views within these pages (Rowling 2001 and response)

The major spawning area for blue grenadier is off the west coast of Tasmania. However, Bruce *et al.* (2001*a*) provide the first evidence of larvae from mainland Australia. Their results indicate that there is a second but limited spawning area in south-eastern Australia. The implications of this for assessment of the fishery (Punt *et al.* 2001*b*) have yet to be considered.

The abundance and distribution of larval blue and spotted warehou are described by Bruce *et al.* (2001*b*). They suggest that there are separate spawning areas for blue warehou in eastern and western regions of the SEF. Similarly to Knuckey and Sivakumaran (2001), they find the timing of spawning varies between regions. For spotted warehou, the picture is less clear, with the data indicating a more continuous link between areas.

Age and growth are crucial inputs to stock assessment. In this issue, the results of two studies are presented. Morison and Rowling (2001) describe age, growth and mortality for redfish. Sex ratios, natural mortality and growth are found to vary between regions. However, because the difference in growth is not consistent between years, they argue that although there is some structuring within the population, the situation is more dynamic than spatially segregated stocks. Jordan (2001*b*) demonstrates that jackass morwong are far older than had been estimated by previous studies, but he reports similar levels of recruitment variability. From trawl surveys off southern and eastern Tasmania, Jordan (2001*c*) finds that jackass morwong abundance varies seasonally at all depths, and that there is distinct size structuring by depth, with juveniles occurring at shallower depths than mature fish. Oceanographic influences on the recruitment of post-larvae are also discussed.

Most of the papers in this section demonstrate the complexity of the SEF, particularly with regard to spatial structure of populations. This has important implications for assessment and management of stocks, which are yet to be fully explored.

Quantitative stock assessment

Surprisingly, few papers dealing with quantitative stock assessment were submitted for this issue. This does not reflect the level of activity in the fishery because assessment is one of the key inputs in the TAC setting process and considerable resources are directed at this area. The primary reason may be one of timing. Aspects of the assessment of two key species, orange roughy and eastern gemfish have been published previously (Smith 1993; Smith and Punt 1998; Punt and Smith 1999), and the assessments of a number of other species are not yet ready for formal publication. Nevertheless, this section provides a useful snapshot of current work.

First, Smith *et al.* (2001) describe the stock assessment process used in the SEF and compare it with that used in other countries. They argue that, although the approach has disadvantages as well as advantages, the latter clearly outweigh the former. Interestingly, Australia appears to be the only country in which fishery managers are active participants in the process.

A primary input to most stock assessment methods is the age composition of the catch. Several methods are available for computing these, but Punt and Smith (2001) demonstrate that assessment and risk analysis may be very sensitive to the method used, particularly for species that show variable growth rates. Another important consideration is selectivity. Cui *et al.* (2001) develop a method of estimating selectivity that allows for variability beyond sampling error. They find that population size-structure and selectivity depend on depth and habitat type, and they discuss the implications of this for future work.

Blue grenadier has become the most important species by size of catch in the SEF. Punt *et al.* (2001*b*) present the first quantitative assessment of this species in Australia. Over 20 years of research and monitoring are synthesized through an 'integrated analysis'. The paper describes how conflicting trends in fishery components are resolved, and the importance of discard data to recruitment estimation is stressed.

The final paper in the issue provides an update on the use of management strategy evaluation (MSE) in the SEF (Punt *et al.* 2001*a*). This approach, likened to use of a 'flight simulator', allows alternative harvest strategies, stock assessment methods, performance indicators and research projects to be compared in relation to achieving management objectives. In terms of stock assessment, it probably represents the way of the future. In the SEF, Punt *et al.* (2001*a*) argue that the lack of clear management objectives and the lack of quantitative assessments for some species are the main challenges to the use of this approach.

Overall, the papers in this section reflect a range of issues associated with stock assessment in the SEF, from a description of the process itself, through key inputs to particular assessments, to new methods for providing advice to decision makers. The papers do, however, reflect the current predominant focus on single species assessments in this multi-species fishery.

Issues for the future

As noted above, the SEF has seen major changes in its 100-year history, in area of operation, industry structure, management and research. As it enters the 21st century, these changes appear set to continue (Table 1). Some of the directions of this change are briefly discussed below, in relation to environmental, management, scientific and industry challenges.

Undoubtedly, the key external challenge to the SEF over the next five years will be in relation to environmental effects of fishing. Clearly, this issue is not limited to the SEF, but the complexity of this fishery will make this challenge all the more difficult to deal with.

Two specific pieces of federal environmental legislation are having an important influence on fisheries in Australia. The first of these is the *Wildlife Protection Act 1984* (WPA), and in particular the decision to remove automatic exemption of commercial fish species under the provisions of Schedule 4 of the Act. This means that fisheries will require approval from the Federal Minister for the Environment to export fish products. The criteria for environmental certification have been developed and are similar in structure to those applied by the Marine Stewardship Council. They require an assessment, not only of the status of the stocks and the sustainability of exploitation, but also of the impact of fishing on the wider ecosystem, including by-catch species, marine habitats and marine food chains. Although some aspects of the wider ecological impacts of fishing have started to be addressed under the ESD objective of the Commonwealth *Fisheries Management Act 1991*, assessment under the WPA is likely to hasten this process and to require more explicit measures to deal with potential adverse ecological impacts.

The second piece of federal environmental legislation that will affect the SEF is the *Environmental Protection and Biodiversity Conservation Act 1999* (EPBCA). This Act brings together a number of facets of environmental legislation, including provisions for endangered species, and will apply to all federally managed fisheries. The EPBCA also requires environmental impacts of fisheries to be assessed, and will audit fishery management plans for compliance with the Act.

The SEF will require environmental certification under both the WPA and the EPBCA. Responses so far have included development of an industry code of conduct and a by-catch action plan. Research projects are underway to study effects of gear (Knuckey *et al.* in press), to improve utilization of by-catch, and to map habitat in the area of the SEF, and at least one no-take MPA has been declared, in an area of sea mounts south of Tasmania. However, little work has been undertaken to look at possible effects of fishing on food chains in the SEF.

Another Federal Government initiative that will affect the SEF is the development of Australia's Ocean Policy (Reichelt and McEwan 1999). A major initiative under the Policy is to develop large-scale Regional Marine Plans (RMPs) based (geographically) on eight identified marine bio-regions. The first RMP to be developed is in the south-eastern area of the EEZ, and is essentially coincident with the area of the SEF. There are still many uncertainties about the form that RMPs will take. What is clear is that they will be based around management of regional marine ecosystems and will deal with multiple uses of the marine environment and interaction between uses. These plans are also likely to incorporate consideration and development of the National Representative System of Marine Protected Areas (NRSMPA).

Several changes in management are already in train over the next five years (Grieve and Richardson 2001). Principal among these is the planned integration of federally managed fisheries in south-eastern Australia under a single management framework. This would bring together the existing trawl, non-trawl and shark fisheries under a single management plan. This will prove challenging for industry as well as for managers, in bringing within a single MAC framework sectors that have traditionally been antagonistic to one another. Aside from amalgamation, the management challenges facing the fishery will include the development of an effective response to the environmental challenge outlined above, developing an appropriate mixture of input and output controls, development of spatial management strategies, and development of agreed harvest strategies for target species (Punt *et al.* 2001*a*). Other key management issues will include the development of effective statutory fishing rights, and containing the costs of management in the face of increasing external demands.

The future scientific issues facing the fishery are reasonably well covered in this journal issue. They include further development and refinement of the Fishery Assessment Group process (Smith *et al.* 2001), development of a programme to obtain fishery-independent abundance data for single-species assessments, and increasing involvement of industry in research and monitoring. The greatest scientific challenge will come from developing a better understanding of the nature of the SEF ecosystem(s), and then developing cost-effective monitoring and assessment tools to manage the effects of fishing on this ecosystem. A starting point will be the identification of robust indicators for ecosystem status and change.

Coping with these challenges and changes over the next decade will require a continuation and strengthening of the partnership approach that has developed between industry, managers, scientists and (increasingly) conservation groups. The particular challenges facing the industry include developing a common identity and purpose across the range of currently disparate sectors, fishing methods and regions, increasing sophistication in dealing with technical scientific issues, and willingness to engage rapidly and effectively in the 'environmental challenge'.

Acknowledgments

We are grateful for financial support from the Fisheries Research and Development Corporation that has made possible the publication of this special issue. We would especially like to thank Ann Grant for her encouragement, support and patience in the development of this issue. We also thank authors and referees for their interest and hard work.

References

Baelde, P. (2001). Fishers' description of changes in fishing gear and fishing practices in the Australian South East Trawl Fishery. *Marine and Freshwater Research* **52**, 411–17.

Bax, N. J., and Williams, A. (2001). Seabed habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring. *Marine and Freshwater Research* **52**, 491–512.

Bax, N. J., Burford, M., Clementson, L., and Davenport, S. (2001). Phytoplankton blooms and production sources on the south-east Australian continental shelf. *Marine and Freshwater Research* **52**, 451–62.

Blaber, S. J. M., and Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345–56.

Bruce, B. D., Condie, S. A., and Sutton, C. A. (2001*a*). Larval distribution of blue grenadier (*Macruronus novaezelandiae* Hector) in south-eastern Australia: further evidence for a second spawning area. *Marine and Freshwater Research* **52**, 603–10.

Bruce, B. D., Neira, F. J., and Bradford, R. W. (2001*b*). Larval distribution and abundance of blue and spotted warehous (*Seriolella brama* and *S. punctata*: Centrolophidae) in south-eastern Australia. *Marine and Freshwater Research* **52**, 631–6.

Bulman, C., Althaus, F., He, X., Bax, N. J., and Williams A. (2001). Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine and Freshwater Research* **52**, 537–48.

Connor, R., and Alden, D. (2001). Indicators of the effectiveness of quota markets: the South East Trawl Fishery of Australia. *Marine and Freshwater Research* **52**, 387–97.

Cui, G., Bax, N. J., Punt, A E., and Knuckey, I. A. (2001). Estimating gill-net selectivity for five species caught in the South East Fishery, Australia. *Marine and Freshwater Research* **52**, 691–9.

Graham, K. J., Andrew, N. L., and Hodgson, K. E. (2001). Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research* **52**, 549–61.

Grieve, C., and Richardson, G. (2001). Recent history of Australia's South East Fishery; a manager's perspective. *Marine and Freshwater Research* **52**, 377–86.

Jentoft, S. (1989). Fisheries co-management: delegating responsibility to fishermen's organisations. *Marine Policy* **13**, 137–54.

Jordan, A. R. (2001*a*). Reproductive biology, early life-history and settlement distribution of sand flathead (*Platycephalus bassensis*) in Tasmania. *Marine and Freshwater Research* **52**, 589–601.

Jordan, A. R. (2001*b*). Age, growth and spatial and interannual trends in age composition of jackass morwong, *Nemadactylus macropterus*, in Tasmania. *Marine and Freshwater Research* **52**, 651–60.

Jordan, A. R. (2001*c*). Spatial and temporal variations in abundance and distribution of juvenile and adult jackass morwong, *Nemadactylus macropterus*, in south-eastern Tasmania. *Marine and Freshwater Research* **52**, 661–70.

Klaer, N. L. (2001). Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. *Marine and Freshwater Research* **52**, 399–410.

Kloser, R. J., Bax, N. J., Ryan, T., Williams, A., and Barker, B. A. (2001). Remote sensing of seabed types in the Australian South East Fishery; development and application of normal incident acoustic techniques and associated 'ground truthing.' *Marine and Freshwater Research* **52**, 475–89.

Knuckey, I. A., Ashby, C., and Moran, T. (in press). Bycatch reduction in Australia's South East Trawl Fishery: letting the message get through, as well as the fish. Proceedings of the Third World Fisheries Congress, Beijing China November 2000.

Knuckey, I. A., and Sivakumaran, K. P. (2001). Reproductive characteristics and per-recruit analyses of blue warehou (*Seriolella brama*): implications for the South East Fishery of Australia. *Marine and Freshwater Research* **52**, 575–87.

Koslow J. A. (1997). Seamounts and the ecology of deep-sea fisheries. *American Scientist* March/April, 168–76.

Koslow, J. A., Bulman, C. M., and Lyle, J. M. (1994). The mid-slope demersal fish community off southeastern Australia. *Deep Sea Research* **41**, 113–41.

Koslow, J. A., Kloser, R. J., and Williams, A. (1997). Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. *Marine Ecology Progress Series* **146**, 21–35.

Larcombe, J. W. P., McLoughlin, K. J., and Tilzey, R. D. J. (2001). Trawl operations in the South East Fishery, Australia: spatial distribution and intensity. *Marine and Freshwater Research* **52**, 419–30.

Mace, P. M. (1997). Developing and sustaining world fisheries resources: the state of the science and management. In 'Developing and Sustaining World Fisheries Resources: the State of Science and Management'. 2nd World Fisheries Congress. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. P. Beumer.) pp. 1–20. (CSIRO Publishing: Melbourne.)

May, J. L., and Blaber, S. J. M. (1989). Benthic and pelagic fish biomass of the upper continental slope off eastern Tasmania. *Marine Biology* **101**, 11–25.

Morison, A. K., and Rowling, K. R. (2001). Age, growth and mortality of redfish *Centroberyx affinis*. *Marine and Freshwater Research* **52**, 637–49.

Pajak, P. (2000). Sustainability, ecosystem management, and indicators: thinking globally and acting locally in the 21st century. *Fisheries* **25**(12), 16–30.

Prince, J. D. (2001). Ecosystem of the South East Fishery (Australia), and fisher lore. *Marine and Freshwater Research* **52**, 431–49.

Prince, J. D., and Griffin, D. A. (2001). Spawning dynamics of the eastern gemfish (*Rexea solandri*) in relation to regional oceanography in south-eastern Australia. *Marine and Freshwater Research* **52**, 611–22.

Punt, A. E., and Smith, A. D. M. (1999). Harvest strategy evaluation for the eastern stock of gemfish (*Rexea solandri*). *ICES Journal of Marine Science* **56**, 860–75.

Punt, A. E., and Smith, D. C. (2001). Assessments of species in the Australian South East Fishery can be sensitive to the method used to convert from size- to age-composition data. *Marine and Freshwater Research* **52**, 683–90.

Punt A. E., Smith, A. D. M., and Cui, G. (2001*a*). Review of progress in the introduction of management strategy evaluation (MSE) approaches in Australia's South East Fishery. *Marine and Freshwater Research* **52**, 719–26.

Punt, A. E., Smith, D. C., Thomson, R. B., Haddon, M., He, X., and Lyle, J. M. (2001*b*). Stock assessment of the blue grenadier *Macruronus novaezelandiae* resource off south-eastern Australia. *Marine and Freshwater Research* **52**, 701–17.

Reichelt, R. E., and McEwan, A. D. (1999). Australia's marine science and technology plan: an action plan for Australia's Oceans Policy. *Marine and Freshwater Research* **50**, 711–16.

Rowling, K. R. (2001). Comment on 'Spawning dynamics of the eastern gemfish (*Rexea solandri*) in relation to regional oceanography in south-eastern Australia'. *Marine and Freshwater Research* **52**, 623–30.

Smith, A. D. M. (1993). Risks of over- and under-fishing new resources. In 'Risk Evaluation and Biological Reference Points for Fisheries Management'. (Eds S. J. Smith, J. J. Hunt and D. Rivard.) *Canadian Special Publication of Fisheries and Aquatic Sciences* **120**, 261–7.

Smith, A. D. M., and Punt, A. E. (1998). Stock assessment of gemfish (*Rexea solandrii*) in Eastern Australia using maximum likelihood and Bayesian methods. In 'Fishery Stock Assessment Models'. (Eds F. Funk, T. J. Quinn II, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan and C. -I. Zhang.) pp. 245–86. Alaska Sea Grant College Program AK-SG-98-01.

Smith, A. D. M., Sainsbury, K. J., and Stevens, R. A. (1999). Implementing effective fisheries management systems – management strategy evaluation and the Australian partnership approach. *ICES Journal of Marine Science* **56**, 967–79.

Smith, D. C., Smith, A. D. M., and Punt, A. E. (2001). Approach and process for stock assessment in the South East Fishery, Australia: a perspective. *Marine and Freshwater Research* **52**, 671–81.

Tilzey, R. D. J. (Ed.) (1994). 'The South East Fishery: a Scientific Review with Particular Reference to Quota Management.' (Bureau of Resource Sciences: Canberra.)

Tilzey, R. D. J., and Rowling, K. R. (2001). History of Australia's South East Fishery: a scientist's perspective. *Marine and Freshwater Research* **52**, 361–75.

Ward, R. D., and Elliott, N. G. (2001). Genetic population structure of species in the South East Fishery of Australia. *Marine and Freshwater Research* **52**, 563–73.

Williams, A., and Bax, N. J. (2001). Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52**, 513–36.

Young, J. W., Bradford, R., Lamb, T. D., Clementson, L. A., Kloser, R., and Galea, H. (2001). Yellowfin tuna (*Thunnus albacares*) aggregations along the shelf break off south-eastern Australia: links between inshore and offshore processes. *Marine and Freshwater Research* **52**, 463–74.

Mar. Freshwater Res., 2001, **52**, 361–75

History of Australia's South East Fishery: a scientist's perspective

R. D. J. Tilzey[A] *and K. R. Rowling*[B]

[A]Bureau of Rural Sciences, PO Box E11, Kingston, ACT 2604, Australia
[B]Fisheries Research Institute, PO Box 21, Cronulla, NSW 2230, Australia

Abstract. The South East Fishery is one of Australia's oldest fisheries. Early research on this trawl fishery centred on tiger flathead, the major target species. In the 1970s, the Federal Government actively encouraged fishery development and funded several trawl surveys. Profitable catch rates and optimistic assessments of resource size caused a rapid expansion of the trawl fleet. Separate jurisdictions hampered strategic approaches to SEF-wide research until 1978. Most SEF research in the mid 1960s to mid 1980s was conducted by State fisheries agencies, but federal involvement increased thereafter. A management shift in 1992 to Individual Transferable Quotas saw stock assessment become the major research priority. Industry involvement in the stock assessment process has increased markedly over the past decade and communication between scientists, managers and industry has improved. Predictive models are still limited by poor biological data for most quota species. Stock assessment uncertainty necessitates the increasing use of risk assessments and management strategy evaluation. Assessment scientists are frustrated by limited resources for research and the perceived reluctance of managers to adopt more precautionary approaches to uncertainty. Since ITQ management, fishing effort has risen significantly and concerns have been expressed about the stock status of several SEF species. Recent federal environmental legislation is now directing more attention towards effects of fishing and resource sustainability issues.

Acronyms

ABARE	Australian Bureau of Agricultural and Resource Economics
AFMA	Australian Fisheries Management Authority
AFS	Australian Fisheries Service
AFZ	Australian Fishing Zone
BRS	Bureau of Rural Sciences, Canberra
CAF	Central Ageing Facility, Victoria
DPFRG	Demersal and Pelagic Fish Research Group
FAG	Fishery Assessment Group
GITLC	Government Industry Technical Liaison Committee
ISMP	Integrated Scientific Monitoring Program
MAC	Management Advisory Committee
SCF	Standing Committee on Fisheries
SCFA	Standing Committee on Fisheries and Aquaculture
SEF	South East Fishery
SEFAG	SEF Assessment Group
SEFRC	South Eastern Fisheries Research Committee
SENTMAC	South East Non-Trawl Management Advisory Committee
SETMAC	South East Trawl Management Advisory Committee
SMP	Scientific Monitoring Program
SRSC	SETMAC Research Sub-Committee
SSF	Southern Shark Fishery

Introduction

The South East Fishery (SEF) is a complex, multi-species demersal fishery encompassing a diverse range of habitats. 'Traditional' SEF trawl management boundaries extend out to the 200 nautical mile (nmile) limit of the Australian Fishing Zone (AFZ) from a line east of Barrenjoey Point, New South Wales (NSW) to a line south from Cape Jervis, South Australia, including waters around Tasmania (Fig. 1). The northern boundary for trawling has recently been extended to 24°35′S to amalgamate what used be known as the East Coast Deepwater Fishery into the SEF. The SEF non-trawl fishery extends from this boundary around to the Western Australia–South Australia border (Fig. 1). The SEF is one of Australia's oldest and most valuable scale-fisheries, traditionally supplying the bulk of fresh fish at the Sydney and Melbourne fish markets. Since the fishery's commencement in 1915, a considerable amount of scientific research has been directed towards it. Although most modern studies are now prompted by periodically reviewed strategic research and management plans for the fishery, early studies were instigated mainly through the initiative of the scientists concerned, acting largely on perceived management needs.

This paper attempts to summarize scientists' past and current perspectives of the fishery. Because the development of the SEF has been accompanied by shifts in research emphasis, an introductory overview of historic

10.1071/MF99185 1323-1650/01/040361

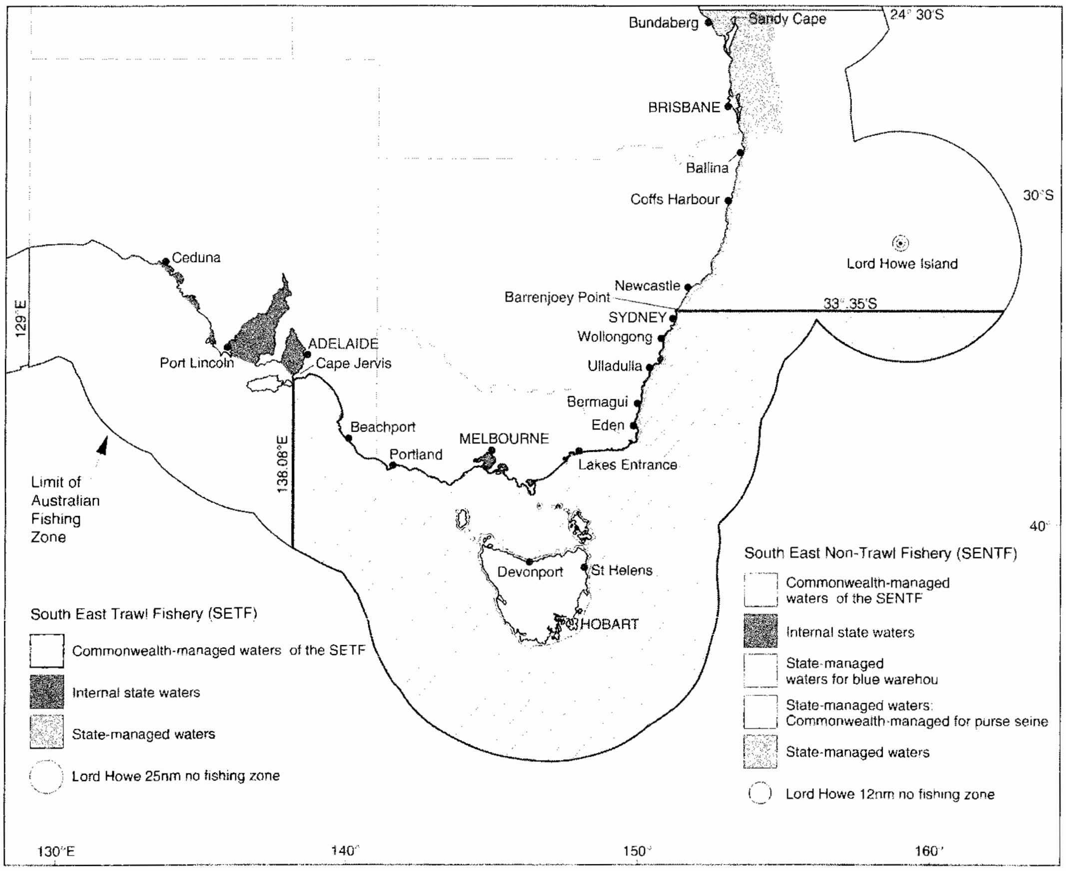


Fig. 1. Management areas of the South East Trawl Fishery and South East Non-trawl Fishery, Australia.

management and research is needed to help explain changes in scientific perspective. Whereas this overview cites numerous references to facilitate the reader's access to such literature, it does not detail the research in question. A large proportion of SEF research has not been formally published in the scientific literature, because it was aimed primarily at providing timely advice to management. The citation of agencies' internal reports and the like reflects this. As there are five governments (Federal, NSW, Victoria, Tasmania and South Australia) involved in managing the SEF or associated inshore fisheries, it is not surprising that several research agencies have been, or are, involved in scientific research on SEF species. Because of numerous historic name changes, fisheries agencies are generally referred to here by their current name only.

Fishery background

Commercial steam trawl operations commenced in 1915 using otter trawl gear (Roughley 1951). From 1915 to the late 1920s, the steam trawl fleet expanded to 17 vessels, with tiger flathead (*Neoplatycephalus richardsoni*) being the principal target species. Fishing grounds were confined to continental shelf waters of <200 m depth and extended from Crowdy Head, NSW, to Gabo Island (Klaer and Tilzey 1996; Klaer 2001). Danish-seine vessels commenced fishing in 1933. As well as being smaller and more economical to operate, Danish seiners were able to exploit inshore fishing grounds too restricted for trawling. Whereas steam trawlers dominated the SEF fleet through to 1950 (Klaer 2001), increasing costs and declining abundance of flathead saw these vessels become progressively phased out during the 1950s and eventually being replaced by much smaller Danish seiners. For a short period in the 1960s the SEF fleet contained only Danish seiners, then the development of the modern, diesel-powered otter-trawl fleet during the late 1960s and early 1970s saw the Danish-seine fleet contract (Rowling 1979). The rapid expansion of the otter-trawl fleet during the 1970s was virtually unfettered by management controls and aided by a generous Federal boat-building subsidy. Thus, fishing capacity in the SEF increased rapidly.

Before the late 1960s, the grounds fished had been virtually confined to shelf waters of <200 m depth. In the 1970s, the fishery expanded to deeper, upper-slope grounds down to about 600 m depth, and progressively southwards to waters around Tasmania and westwards into western Bass Strait. A review of the status of the 'trawl and Danish seine' fishery in 1982 found that about 180 vessels were operating in either a full-time or a part-time capacity. Nevertheless, the fishery was still considered to be 'under-exploited' (Graham *et al.* 1982) and the waters south and west of Bass Strait to be 'undeveloped'. The development of a fishery for blue grenadier (*Macruronus novaezealandiae*) in the mid 1980s and the subsequent development of an orange roughy (*Hoplostethus atlanticus*) fishery saw a pronounced shift in fishing effort away from the 'traditional' area off NSW to deeper (>600 m) southern waters. This was accompanied by a decline in the number of small (<25 m length) trawlers and an increase in the number of larger vessels. Despite a reduction in overall vessel number, total fleet tonnage and horsepower increased. In December 1991, just prior to the introduction of an Individual Transferable Quota (ITQ) management regime, the SEF trawl-sector fleet consisted of 105 trawlers and 30 Danish seiners (Tilzey 1994). Since ITQ management, the Danish-seine fleet has pooled most of its quota and operates independently from the trawl fleet. Tilzey (1994) summarized the development of the trawl sector in more detail. Across the fishery, quota has also gradually become aggregated on to fewer vessels. In 1999, 89 trawlers (including 3 chartered freezer-trawlers) and 20 Danish seiners operated in the fishery.

Although the SEF was called the South East Trawl Fishery until 1992, many non-trawl fishers have traditionally fished for some of the same target species in SEF waters. Hook-and-line methods and gill-netting were used in coastal waters long before trawling commenced. Drop-lining, demersal long-lining, trapping and demersal gill-netting are now the main fishing methods used in the non-trawl sector. The 1992 change of the fishery's name to the SEF acknowledged that it was not solely composed of trawlers and Danish seiners. Non-trawl boat numbers in Federal waters were unregulated until 1985, when a freeze was put on issuing new licences. By this time a large number of fishers (>2000) held such licences. In 1988, gill-net fishers with Southern Shark Fishery (SSF) endorsements were placed under input management controls (gear units) applying to all Federal waters. Further rationalization of the non-trawl fishery occurred in 1992 when the number of permits to take demersal scalefish in Federal waters was fixed at about 550. Following the introduction of more prescriptive access criteria, the number of federally endorsed non-trawl operators in April 1998 had been reduced to 151. However, there are also numerous additional State-endorsed fishers who catch some SEF species under State jurisdiction. Many SEF operators also have endorsements in other federally managed fisheries that share waters with the SEF, namely the SSF, Bass Strait Central Zone Scallop Fishery and the Eastern Tuna and Billfish Fishery. SEF fishers often also hold endorsements in fisheries under State jurisdiction. Although there are significant interactions between these fisheries and the SEF, particularly in the cases of the SSF and some State fisheries, these fisheries are managed as separate entities.

Jurisdictional and management background

Historic SEF research should be viewed in the context of the prevailing jurisdictional and management arrangements of the time. Harrison (1991) described the Federal Government's role in Australian fisheries and noted that, although the Constitution gave responsibility for fisheries in Australian waters beyond 'territorial limits' to the Commonwealth of Australia, there was no significant federal fisheries legislation until *The Fisheries Act 1952*. Before 1952, the States controlled 'extra-territorial' fisheries on behalf of the Commonwealth of Australia and there were no legal impediments restraining fishers' movements in such 'extra-territorial' waters. After 1955, the parallel application of State and federal legislation gradually resulted in major jurisdictional and administrative conflict. This continued until 1978 when the High Court endorsed a political solution to this problem — the *Offshore Constitutional Settlement* — that enabled assignment of State, federal or joint jurisdiction on the basis of individual fisheries rather than the boundaries of State or federal-controlled areas. Early efforts to develop a national fisheries policy were continually frustrated by parochialism, as were co-operative research proposals between the (then) Commonwealth Department of Primary Industry (DPI), the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and south-eastern State fishery authorities. It was not until 1961, largely at the prompting of CSIRO's Geoffrey Kesteven, that the Standing Committee on Fisheries (SCF), a national committee comprising State and federal Directors of Fisheries, reached general agreement that stock assessment was a pre-requisite to effective management. Paradoxically, the 1960s saw a marked decrease in CSIRO's fisheries capabilities (see below).

Despite considerable efforts by the Commonwealth DPI and CSIRO in the early 1960s to foster co-operative research projects and to more effectively integrate Australian fisheries administration, parochial attitudes persisted. The SCF's Southern Pelagic Project Committee, a committee formed in 1961 to assist management of southern Australian fisheries, largely focussed on the southern bluefin tuna (*Thunnus maccoyii*), southern rock lobster (*Jasus edwardsii*), Australian salmon (*Arripis trutta*) and scallop (Pectinidae) fisheries. The trawl fishery received scant attention. Efforts to form a South Eastern Fisheries Research Committee (SEFRC) in 1964 were frustrated by NSW and the matter was dropped until 1968, when a South Eastern Fisheries Committee (SEFC) was finally formed

(Harrison 1991). The SEFC was given responsibility for the co-ordination of management and associated research in south-eastern Australia and it played a major role in the practical management of fisheries throughout the 1970s. One of the early SEFC initiatives was to establish the Demersal and Pelagic Fish Research Group (DPFRG) in 1975. However, inter-State political issues still dominated SEFC debate and SEFC was abandoned by the SCF in 1987 when the more research-centred SEFRC was eventually formed.

The 200 nmile AFZ became operational in 1979, greatly expanding the federal area of jurisdiction. This prompted the Commonwealth DPI to enter into a formal agreement with CSIRO to provide the DPI with the information needed for management. DPI and CSIRO made a joint Cabinet submission that resulted in funding for 24 additional CSIRO staff and the charter of a 50 m stern trawler and about 18 DPI positions for AFZ work. Also, the Australian Fishing Zone Information System, an integrated data repository for information on operators, catch, effort, etc., was created. Some of this AFZ research effort was to be directed towards the SEF, but CSIRO's attempt to instigate a multi-species study centring on this fishery was vigorously opposed by NSW and the study was eventually relocated to the North West Shelf (e.g. Sainsbury 1988). NSW viewed this study as duplicating research being carried out by their FRV *Kapala*. It was not until 1984 that CSIRO recommenced biological research on SEF species. The failure of CSIRO to provide research support to the SEF from the mid 1960s to mid 1980s resulted in the States (principally NSW) assuming prime responsibility for stock assessment and advice on fisheries management and expanding their activities in this area during this period.

On a national basis, DPI recruited more biologists to meet its need for immediate advice. The increasing economic input into management saw fisheries economists relocated into the Australian Bureau of Agricultural and Resource Economics (ABARE) in 1982. The establishment of the Bureau of Rural Sciences (BRS) in 1986 included the fisheries resource biologists from DPI. The BRS role was to supply independent scientific advice on fisheries matters to the DPI and the Federal Minister responsible for fisheries. A major federal fisheries policy statement was released in 1989 (DPIE 1989). This flagged the creation of a statutory body, eventually the Australian Fisheries Management Authority (AFMA) created in 1992, to assume federal fisheries management responsibilities. Grieve and Richardson (2001) have summarized recent SEF management actions.

Before the mid 1980s, the perspectives of most SEF scientists were somewhat narrow. Nearly all research was State-based and aimed only at species of commercial importance to the State in question. Single-species studies were common. Despite the efforts of groups such as the SEFRC and DPFRG, most research was conducted in isolation from that in other States. After the Federal Government introduced a management plan and established the South East Trawl Management Advisory Committee (SETMAC) in1985, a more fishery-wide approach to research was gradually adopted. It should be stressed that the introduction of ITQ management in 1992 led to a major shift in research emphasis towards stock assessment. SEF research priorities are now largely management-driven by AFMA and the associated MACs. Recent environmental legislation such as the inclusion of fish in the *Wildlife Protection (Regulation of Exports and Imports) Act 1982* and the new *Environment Protection and Biodiversity Conservation Act 1999* has also resulted in Environment Australia becoming involved in reviewing the long-term sustainability of fisheries such as the SEF.

Research history

The steam trawl and Danish-seine era (1915–70)

The first scientific investigations into south-eastern demersal fisheries were the exploratory surveys carried out by Dannevig (then the Federal Director of Fisheries) on the trawler *Endeavour* (Dannevig 1913); these preceded the development of commercial fishing. Following the loss of the *Endeavour* with all hands in 1914, virtually no 'field' studies were conducted during the following two decades. Tiger flathead was the principal target species for steam trawlers. A decline in this fishery prompted Colefax of the University of Sydney to investigate this species on a part-time basis during the 1930s (Colefax 1934, 1938). Flathead ageing was also carried out at the Australian Museum (Dakin 1939). However, it was not until the formation of the CSIRO (at that time the Council for Scientific and Industrial Research) Fisheries Section in 1937 that fisheries research on a 'full-time' basis commenced, albeit with very limited resources. Most of CSIRO's initial research projects were directed towards pelagic fisheries development and oceanographic studies, and only comparatively limited research was carried out on demersal fish stocks. SEF research during this period again largely centred on tiger flathead. Fairbridge (1948, 1950, 1951*a*, 1951*b*, 1952*a*, 1952*b*) studied this fishery and found it to be in significant decline, following a partial recovery during the period of the Second World War. Houston (1955) also reviewed the status of the NSW trawl fishery in the early 1950s. Blackburn (1978, 1979) summarized much of the catch composition data collected from the mid 1940s to mid 1960s. With the continued decline of the tiger flathead fishery, increased landings of jackass morwong (*Nemadactylus macropterus*) and redfish (*Centroberyx affinis*) were made by SEF vessels, but little biological research was conducted on these two species. During the 1940s, barracouta or 'snoek' (*Thyrsites atun*) comprised Australia's largest finfish fishery, and much research effort was directed towards this species

(Blackburn 1949, 1950, 1957, 1960; Blackburn and Gartner 1954; Grant *et al.* 1978). However, barracouta were caught mainly by an inshore trolling fleet off western Victoria, and since this fishery virtually ceased in 1975 barracouta has been only a low-value by-catch in the SEF. Following the demise of the steam trawl fleet, SEF research virtually ground to a halt. Thus, during this pre-1970s era, tiger flathead was the only current SEF quota species to receive significant research attention. Economic research was in its infancy (e.g. Lorimer and Barker 1967).

The 1960s also saw a marked decline in fisheries research by CSIRO. The departure of their leading fisheries scientist Geoffrey Kesteven to Mexico saw George Humphries, Division Chief from 1956 to 1971, scale down fisheries programmes in favour of oceanographic investigations. During this period, several fisheries scientists left CSIRO and joined State fisheries agencies. A mathematician appointed by CSIRO to analyse SEF trawl and Danish seine data did not complete this task before departing overseas. Thus, 'hands-on' SEF research became almost solely State-based.

The 'new development' era (1970–90)

The rapid expansion of the SEF otter-trawl fleet was facilitated by government policies aimed at 'developing' Australia's fisheries. Before and after the creation of the 200 nmile AFZ in 1979, a considerable amount of federal research funding was provided to south-eastern fisheries agencies for exploratory fishing and trawl surveys of SEF upper-slope waters. The principal objectives of this research were to identify trawl grounds and evaluate the potential of demersal fish resources. CSIRO carried out several midwater and demersal trawl surveys in SEF waters with the FRV *Courageous* during the mid 1970s. At the same time, a joint Tasmania—Commonwealth of Australia project chartered the commercial trawler *Zeehan* to survey shelf waters around Tasmania. NSW's FRV *Kapala* tested midwater trawling in the early 1970s and conducted stratified random demersal trawl surveys of NSW and north-eastern Bass Strait waters in 1976–78 and 1980–81. These surveys were documented in a long series of *Kapala* Cruise Reports published by the NSW Fisheries Department. Victorian research on SEF species effectively began in the mid 1970s with trawl survey work off Portland by FRV *Sarda*. This was followed by a more extensive four-year (1982–85) survey of eastern Bass Strait by FRV *Sarda* (to 440 m depth) and (CSIRO's) FRV *Soela* (to 800 m depth), which reported the distribution, abundance and biomass of 37 species by depth and season (e.g. Wankowski and Moulton 1986). A similar survey of western Bass Strait was later conducted in 1987–90, using chartered commercial vessels (Smith *et al.* 1995*a*). Tasmania conducted a major trawl survey programme off southern Australia between 1981 and 1985. These surveys provided information about the distribution and abundance of several deepwater species, including blue grenadier (Wilson 1981, 1982*a*) and orange roughy (Wilson 1982*b*, 1984). Also, a few foreign vessels were allowed access to the AFZ. Collins and Baron (1981) described exploratory demersal and pelagic trawling carried out by a Polish vessel in southern SEF waters during 1979–80. Following industry's discovery of commercial quantities of orange roughy, both Tasmania (Lyle *et al.* 1991) and CSIRO (Bulman and Koslow 1991; Koslow *et al.* 1994*a*) undertook trawl surveys in the late 1980s, primarily aimed at estimating orange roughy abundance, and the reproductive biology of orange roughy was also studied (Bell *et al.* 1991).

The development of significant fisheries for many SEF species saw increases in targeted research on many of the species concerned. The central core of NSW-based SEF research was the 'Danish Seine and Otter Trawl Program' that ran from the mid 1970s to the early 1990s. This program, jointly funded by the NSW and federal governments, focussed on monitoring commercial catch compositions of the major trawl species. It also conducted sequential studies of the biology and population dynamics of tiger flathead (Montgomery 1985), jackass morwong (Smith 1982, 1983), redfish (Diplock 1984; Rowling 1990*b*), gemfish (Rowling 1990*a*; Rowling and Reid 1992), the ocean perch *Helicolenus percoides* and *H. barathri* (Park 1994) and the royal red prawn *Haliporoides sibogae* (Baelde 1991, 1992, 1994). FRV *Kapala* was involved in targeted studies on gemfish, redfish and school whiting (*Sillago flindersi*). Tasmania collected biological and fishery data between 1979 and 1987 by research trawling and commercial catch sampling, and much of this work was documented and analysed by Ford and Lyle (1992). CSIRO again became involved in SEF research. The FRV *Soela* began a southern-temperate-fish programme in 1984, aimed at describing fish resources below the 450 m isobath (Blaber 1984; May and Blaber 1989; Young and Blaber 1986; Young *et al.* 1987). CSIRO then began investigations into the developing blue grenadier fishery (Bulman and Blaber 1986; Kenchington and Augustine 1987; Milton and Shaklee 1987; Bruce 1988; Gunn *et al.* 1989; Kenchington 1989; Thresher *et al.* 1989). Tasmania also conducted age-and-growth studies on the blue grenadier fishery between 1984 and 1986 and an estimate of natural mortality was obtained (Evans 1986).

The introduction of a compulsory, shot-by-shot logbook system for the trawl and Danish-seine fleets in October 1985 greatly improved the quality of catch-and-effort data. Prior to this logbook, State agencies had used catch-recording systems of varying detail, with little standardization among agencies. During this era, DPFRG played an increasingly major role in forging strong links among fisheries agencies on SEF research issues. DPFRG comprised scientists from each of the four south-eastern States, CSIRO and the

Commonwealth of Australia. DPFRG regularly held 'trawl' workshops to facilitate, coordinate and review research into the demersal fisheries of south-eastern Australia. BRS also became involved in coordinating SEF research (e.g. Williams 1989) and began analysis of the SEF logbook database (Tilzey *et al.* 1990). Targeted economic research also began in this era. DPI conducted economic surveys of the fishery from 1972/73 to 1980/81 (Anon. 1978; Jarzynski 1980; Menz *et al.* 1986) and conducted another survey and an economic analysis of management options for the fishery in 1987–88 (Anon. 1989).

The modern, 'stock assessment' era (1990 onwards)

The new policy statement for federal fisheries management (DPIE 1989) and the arrival of AFMA as an independent federal fisheries manager heralded the adoption of science-based management policy in the SEF. Also, SETMAC was streamlined and given an independent Chair and *Offshore Constitutional Settlement* agreements with the adjacent States gradually ceded control of major SEF trawl species to the Federal Government. The shift to output management controls for the SEF created an increasing need for resource assessment to support the process of setting TACs. The Australian Fisheries Service (AFS, the fisheries arm of DPI), followed by AFMA, actively sought scientific advice for the declining gemfish and developing orange roughy fisheries, then for other SEF species for which ITQ management was planned. Because of the similarity between some SEF and New Zealand demersal fisheries, ABARE and BRS convened a Southern Trawl Fisheries Conference in 1990 (Abel *et al.* 1991) to encourage cooperative research between these two countries. From 1991 onwards, DPFRG's research review role was largely supplanted by the need to carry out 'hands-on' stock assessment workshops. In 1992, DPFRG identified research priorities and drew up the initial strategic research plan for the SEF. One of this plan's recommendations was the formation of a formal Stock Assessment Group to conduct the annual scientific assessment of quota species to assist the TAC review process. The subsequent formation of the SEF Assessment Group (SEFAG) in 1993 coincided with disbanding of the DPFRG by the Standing Committee on Fisheries and Aquaculture (SCFA). SEFAG reports directly to AFMA, as well as to SETMAC.

The early 1990s also saw increasing direct interaction between scientists and industry. SETMAC became directly involved with research through the establishment of a Government Industry Technical Liaison Committee (GITLC) in 1989 to facilitate scientific evaluation of the orange roughy fishery. A major initiative of GITLC was endorsement of the principle of using 'quota-for- charter' for research projects and this greatly expedited research on deepwater species. SETMAC also established a Gemfish Liaison Committee to assist the management of the declining eastern gemfish fishery. Both industry representatives and scientists regard these committees as being successful in improving communication between the two groups (Ross and Smith 1997), but both committees were short-lived. They were disbanded following the formation of the SETMAC Research Sub-Committee (SRSC) and SEFAG in 1993, because both new groups had adequate industry representation to ensure the dialogue continued. The role of the SRSC was to annually recommend to SETMAC a set of research priorities for the fishery.

The central role of SEFAG was and is to undertake the stock assessment analysis required by SETMAC, the recently formed South East Non-Trawl Management Advisory Committee (SENTMAC) and AFMA and report on stock status. The Group comprises scientists from the State fisheries agencies, ABARE, BRS, CSIRO and a conservation agency, AFMA managers, and trawl and non-trawl industry members. Since 1994, the Group has produced annual Fishery Assessment Reports that include summaries of the status of all quota species (Staples *et al.* 1994; Staples and Tilzey 1995; Chesson 1996, 1997; Tilzey 1998, 1999). The Group produced individual assessment reports for all SEF quota species in 1994. Since then, these reports have been revised on a periodic basis. Species-specific assessment workshops were held when management problems or new information warranted such a forum. The continued decline of the eastern gemfish fishery focussed much assessment effort thereon and led to the formation of a specific Eastern Gemfish Assessment Group. The success of this group, particularly in resolving differing perspectives between scientists and industry, led to the creation of specific assessment groups for blue grenadier, blue warehou, orange roughy and redfish. Recent assessment procedures have often extended beyond estimation of resource status to developing risk-assessment methods, harvest strategies and evaluation of management strategies (e.g. Smith and Punt 1998; Punt and Smith 1999*a*, 1999*b*; Smith *et al.* 1999). However, whereas >100 species are regularly landed by SEF fishers, periodic assessments are limited to quota species only. In 1998, non-quota species comprised 19% by weight of the total landed catch of the fishery (Tilzey 1999).

Another major step towards facilitating regular stock assessments was the establishment in 1991 of a Central Ageing Facility (CAF), based at the Marine and Freshwater Resources Institute, Victoria. The CAF became the primary source of age and growth data for selected SEF species for which a validated technique was available, and it developed ageing techniques for others (Smith and Stewart 1994; Smith *et al.* 1995*b*). Morison *et al.* (1998) summarized the methods used. For each species, the CAF produces reports that include mean length-at-age, growth parameters and age–length keys (e.g. Morison 1996; Morison *et al.* 1999).

SEFAG now determines the schedule for ageing individual SEF quota species.

Because of the lack of information on discarding practices and the limited availability of fish size/age data, SEFAG flagged the need for a structured onboard and port-based catch- monitoring program. A Scientific Monitoring Program (SMP) was subsequently established in 1993 to collect information on total catch composition and fishing practices (e.g. targeted species and quantitative composition of retained and discarded catches). Initially, the SMP complemented a NSW-based bycatch monitoring study (Liggins 1996). Acknowledging a continuing need to collect these important data and a need to integrate activities, an ongoing Integrated Scientific Monitoring Program (ISMP) replaced the SMP in 1997 (Smith *et al.* 1997). Information collected across the fishery includes shot-by-shot species composition, catch weights and sizes for both retained and discarded species, details of fishing practices and otoliths for the CAF (Knuckey *et al.* in press). For non-quota species, ISMP data represent virtually the only information available.

As well as input from the CAF and the SMP/ISMP, various research projects conducted by CSIRO, BRS and State agencies provided crucial input to the stock-assessment process. The advent of *Offshore Constitutional Settlement* arrangements, which gave the Federal Government jurisdiction over major SEF species, saw State-funded research decline and federally funded research increase. BRS continued spatial analyses of the SEF logbook database to examine the structure of the fishery (Klaer and Tilzey 1994) and has extended this work using Geographic Information System methodology (Larcombe *et al.* 2001). Economic research continued. In 1989/90, ABARE commenced regular surveys aimed at assessing SEF economic performance and published as a series of fishery survey reports (e.g. Brown 1997). Targeted ABARE studies included those on by-catch management options (Baulch and Pascoe 1992), fish marketing (Smith *et al.* 1998*b*) and quota trading (Hogan *et al.* 1999). Economic data continue to be collected on fish prices, costs and returns from fishing, and the economic structure of the SEF.

Following the purchase of the FRV *Southern Surveyor* in 1991, CSIRO increased its research on SEF deepwater species, particularly on developing acoustic methods for estimating biomass. Several acoustic surveys of orange roughy in the 'St Helens' spawning aggregation off eastern Tasmania and aggregations on seamounts off southern Tasmania were conducted, with trawling being used only to assess the species composition of 'marks' (Elliot and Kloser 1991; Kloser 1996; Kloser *et al.* 1996, 1997). Egg-production surveys were also used to estimate orange roughy biomass of the 'St Helens' spawning aggregation (Bulman and Koslow 1995; Koslow *et al.*1995*a*, 1995*b*). These studies formed the primary basis for setting TACs for the eastern and southern orange roughy management zones. Much of this survey work was carried out in conjunction with industry vessels, the latter undertaking the requisite trawling and also acting as research platforms on a quota-for-charter basis. Underwater photography was tested as a method to identify fish marks in the water column (Koslow *et al.* 1995*c*; Koslow 1996). Acoustic surveys of orange roughy have continued, with the most recent being conducted during the 1999 winter. With increasing development of the winter blue grenadier fishery off western Tasmania, CSIRO research was again directed at this species. Both acoustic and egg production surveys were used to estimate the spawning biomass of blue grenadier (Bulman *et al.* 1999; Koslow *et al.* 1994*b*).

Considerable CSIRO research effort was also directed towards orange roughy stock discrimination (Elliott and Ward 1991; Elliott *et al.* 1995; Thresher *et al.* 1999). Other studies of stock structure included those on blue-eye trevalla (Bolch *et al.* 1993, 1994; Ward and Last 1993) and oreos (Oreosomatidae) (Elliott *et al.* 1998; Ward *et al.* 1996, 1998). CSIRO has also conducted taxonomic research and produced identification guides for SEF species (Last *et al.* 1981; Last and Stevens 1994; Daley *et al.* 1997, 1998; Yearsley *et al.* 1999). Other studies include those on fish larvae (Bruce *et al.* in press, 2001*a*, 2001*b*).

State agencies also continued SEF research, albeit largely with federal funding. Research conducted at the Australian Museum clarified the stock structure of gemfish and ocean perch (Paxton and Colgan 1993; Colgan and Paxton 1997). A NSW study assessed trawl by-catch and associated discarding practices over 1993–95 (Liggins 1996). Trawl surveys by the FRV *Kapala* in 1996–97 replicated those of 1976–77 and provided fishery-independent information on the changes in relative abundance and size composition of commercial fishes that have occurred over this 20-year period (Andrew *et al.* 1997). Ongoing NSW projects include monitoring of the eastern gemfish fishery and the blue-eye trevalla dropline fishery (Rowling 1996, 1999) and the development of stock assessments for redfish (Rowling 2001) and silver trevally *Pseudocaranx dentex* (Rowling and Raines 2000). Victoria undertook targeted studies on blue warehou and spotted warehou (*Seriolella punctata*) (Smith *et al.* 1994; Knuckey and Sivakumaran 1999, 2001; Knuckey *et al.* 1999) and orange roughy (Smith *et al.* 1988*a*; Knuckey and Smith 1997). During the early 1990s, Tasmania investigated the Tasmanian fishery for blue-eye trevalla (Baelde 1995, 1996) and conducted trawl surveys of shelf and inshore fish resources (Jordan 1997). More recent Tasmanian studies include those on the jackass morwong (Jordan 2001*a*, 2001*b*) and sand flathead (*Platycephalus bassensis*) (Jordan 2001*c*) fisheries.

The consolidation and implementation of Ecologically Sustainable Development and other environmental legislation, together with increasing public concern about the effects of fishing, have also seen a shift towards more holistic 'ecosystem' research. CSIRO studied the trophodynamics of the shelf/slope ecosystem supporting orange roughy and other mid-slope fisheries south of Australia (Koslow 1996; Parslow et al. 1996; Koslow *et al.* 1997). Another CSIRO study on seamounts south of Tasmania led to the proclamation in 1999 of one of the world's first deepwater marine reserves (Koslow and Gowlett-Holmes 1998). CSIRO also studied SEF shelf waters off eastern Victoria and southern NSW to determine the sources of production that fuel the SEF ecosystem (Bax *et al.* 1999*a*, 2001; Bax and Williams 2000; Bulman *et al.* 2001). Research was subsequently focussed on the importance of habitat to fisheries production (Bax *et al.* 1999*b*) using towed camera systems (Barker *et al.* 1999) and acoustic techniques (Kloser *et al.* 2001). These techniques were used together with detailed maps from local fishers to develop comprehensive descriptions of the major shelf habitats (Bax and Williams 2001), and the fish communities thereon (Williams and Bax 2001). Morphologic characters of individual species were used to determine ecological similarities between different fish communities occurring in similar habitats (Bax *et al.* 1999c). One key habitat attribute determining fish distribution was depth, and the potential for managing fishing effort by depth to reduce by-catch of juvenile flathead was explored (Bax 1997).

The scientific perspective

Beginning with Dannevig (1913), much of the SEF research effort before the mid 1980s was directed towards exploratory trawl surveys aimed at developing the fishery. Any biological studies were centred on the dominant tiger flathead fishery of the steam trawl era and were largely prompted by the decline of this fishery. Following the scientific perception of the time, that a fish should be allowed to spawn at least once prior to capture, the minimum legal (codend) mesh size (90 mm) for the fishery was based on the size at maturity of tiger flathead. Despite the multi-species nature of the modern trawl fishery and significant onboard discarding of some commercial species, this mesh-size requirement is still enforced. Mesh selectivity studies only recommenced in 1999. The late 1940s saw increasing recognition of the importance of gathering information on trends in the size structure of the commercial catch, and periodic fish measuring was introduced at the Sydney Fish Market (e.g. Blackburn 1978). Catch rates were also being used to determine trends in the flathead fishery, although the units of effort (trawler days) were crude. In the absence of clear management objectives for the SEF, scientists were expected to make management recommendations. Whereas a few scientists were becoming familiar with the mathematical stock modelling approaches pioneered by Beverton and Holt (1957), there was no commitment to applying these to the SEF.

The new wave of exploratory trawl surveys that accompanied the expansion of the SEF fleet in the late 1970s and early 1980s provided standing-crop estimates derived from area-swept techniques. These estimates involved several assumptions about gear efficiency and fish catchability and were acknowledged to lie within wide confidence bounds. Nevertheless, the main findings of these surveys pointed to substantial virgin resources on the continental slope and encouraged industry investment in the fishery. Comparatively few scientists advocated caution concerning the size of fish resources. The development of the eastern gemfish fishery in the late 1970s saw a rapid increase in the capacity of the NSW trawl fleet. Optimistic estimates of the available trawl resources and the Federal Government's developmental philosophy and boat-building subsidy then saw the trawl fleet expand southwards. Although concern about over-capitalization resulted in input management controls being introduced into the SEF in 1985, the south-west sector of the fishery was routinely characterized by scientists as being under-exploited until the late 1980s. Indeed, poorly substantiated and sometimes overly optimistic predictions of the size of the newly discovered orange roughy resource off eastern Tasmania, combined with the extraordinarily high catch rates attained from fishing of spawning aggregations of this valuable species, precipitated significant further investment in the fishery.

The targeted biological research carried out by State fisheries authorities during the mid 1970s to mid 1980s largely focussed on fish species of local commercial importance. In the absence of specific management objectives, research priorities were driven largely by the scientists' perceptions of fishery management needs. Consequently, most research was aimed at gathering basic biological and fishery parameters, albeit for a limited range of species. In most instances, the acquisition of the scientific knowledge needed to manage these fisheries on a sustainable basis lagged well behind their rapid development. Initially, there was very little co-ordination among States, but a more fishery-wide approach to management and research was gradually adopted, with the DPFRG becoming increasingly prominent in research co-ordination. However, it was not until the South East Trawl Management Plan was introduced in 1985, that federal agencies (principally CSIRO and BRS) became more directly involved in SEF biological research. The application of population modelling to SEF species was still in its infancy and it was not until the late 1980s that techniques such as cohort analysis were used (e.g. Allen 1989). In the late 1980s and early 1990s, the 'high-priority' gemfish, blue grenadier and orange roughy fisheries absorbed most of the research and assessment effort, and other important developing fisheries such as those for ling, blue and spotted warehou and deepwater sharks consequently received little research attention.

The adoption in 1992 of ITQ management for the SEF trawl sector saw a quantum shift towards the involvement of AFS/AFMA and SETMAC in setting research priorities. Quantitative stock assessment of the 16 quota species or species-groups became an important management and scientific objective. Fisheries scientists had previously cautioned managers that there was inadequate information upon which to base most TACs, and a DPFRG workshop held in 1991 was able to provide AFS/AFMA with yield estimates for only 5 of the 16 quota species. The initial TACs for the other 11 species were subsequently based on historic catch trends only. Although trends in catch rates were used as a prime indicator of stock status, DPFRG stressed that such trends should be viewed with caution because of unknown shifts in fishing power and fishing behaviour. Most scientists distanced themselves from the formal TAC-setting process and the heated debate that often accompanied the 'trade-off' between conflicting socio-economic and stock-conservation needs. Resolving such dispute was perceived to be solely the responsibility of SETMAC and AFS/AFMA, and scientists generally did not wish to compromise their independent 'scientific integrity' through involvement. Simultaneous communication among scientists, managers and industry was limited.

Ineffective communication contributed to scientific estimates of stock status being frequently disputed, especially if they appeared likely to result in a lower TAC. Scientists were periodically called on to formally present their results to industry, but there were few avenues for direct industry input into the assessment process. In general, scientific data used as a basis to recommend reduced TACs were subject to greater scrutiny than those used to increase TACs, and there was inevitably a greater time-lag in the adoption of 'unfavourable' stock assessments. Industry and AFMA subjected a key orange roughy assessment to external review by overseas experts. Despite the facilitation by AFMA and SETMAC of annual industry workshops that were open to all and were intended in part to discuss scientific issues, socio-economic management issues dominated debate (e.g. Nicoll 1993*a*, 1993*b*). Although industry had become formally involved in scientific debate following the creation of SETMAC's technical liaison committees from 1989 onwards, it was not until the SEFAG was established by AFMA in 1993 that a much more effective and widespread communication process began.

The establishment of SEFAG and the subsequent creation of specific Fishery Assessment Groups (FAGs) resulted in important changes in the way that SEF science was conducted. The groups involved industry and managers in a direct and ongoing input to the stock-assessment process. Furthermore, by embracing a number of scientists (including industry-based scientists), they established a structured process of broader scientific input to assessments prior to formal peer review. Where pertinent, New Zealand scientists have also attended FAG meetings. Consequently, the quality and acceptance by industry and managers of stock assessments has generally improved. Communication among scientists, industry and managers has also improved as a greater measure of mutual trust has developed. For species that have properly functioning FAGs, industry's understanding and acceptance of results have greatly improved. The targeted inclusion on a FAG of industry members from different areas or sectors of the fishery has allowed a wider range of stock hypotheses to be tested and has given industry the chance to view data and hear reports from other areas, promoting a fishery-wide view of events. FAGs also give fishers a chance to comment 'in-camera'. Because stock assessments are linked to TAC levels, fishers are generally reluctant to publicly comment on declining catches or other negative indicators.

The evolution of the communication process is well illustrated by events in the eastern gemfish fishery where initial assessments of decline (Rowling 1987) were subject to considerable criticism (Rowling 1997), but there is now general acceptance by most industry sectors of the stock's over-fished status. Smith *et al.* (1999) summarized the key events in this fishery that led to this change in industry perception. However, their brief summary diplomatically avoided describing industry's great hostility to initial gemfish assessments and the ongoing reluctance by a few fishers to accept current assessments of stock decline.

Notwithstanding the development of increasingly sophisticated predictive models for major SEF quota species, developing adequate abundance indices for use by these models is still a significant problem. Stock assessments are still heavily reliant upon fishery-dependent information, and fishery-independent estimates of absolute, or comparative, abundance are available for a few species only. Attempts to develop standardized catch-rate indices have been largely confounded by changes in the SEF fleet's fishing practices, despite efforts to quantify such practices (Prince *et al.* 1998). The poor knowledge of many population parameters has led to the increasing use of risk-assessment models for major species, to help management cope with uncertainty. Orange roughy was the first fishery (albeit one with a fishery-independent abundance index) to be assessed in this manner and the risks associated with a range of catch levels against holding the exploited biomass at levels of 20% and 30% of virgin biomass were estimated. For some species that are known to have wide variations in recruitment, the risks associated with different harvest strategies are now estimated (e.g. Punt and Smith 1999*b*). Another important science-driven advance has been the development of a framework for management strategy evaluation, which facilitates dealing with multiple management objectives and uncertainties in prediction (Smith *et al.*1999). For many species modelling is now much more geared to evaluating management options, albeit within an output control framework.

With AFMA and its associated committees now directing much of SEF research, some scientists are concerned about reduced autonomy, the increasing focus on single-species stock assessment and excessive industry influence on assessments and research priorities. However, some (probably most) are supportive of the more open assessment process and value industry information and the opportunities for detailed discussion with managers and industry. In addition, the involvement of 'conservation' members on MACs and FAGs has to some extent eased the demands on scientists as advocates for a precautionary management approach. The ISMP is now funded largely by means of an industry levy, and the increasing use of industry vessels for dedicated research purposes has been more cost-effective than using dedicated research vessels. There are scientific concerns about the lack of ownership of the assessment process and SEF research in general, because there is currently no long-term agency commitment to archiving research data and providing 'core' research funding. Most SEF research is dependent upon the ability of research agencies to obtain 'external' funding, with most research projects extending over a mere 1–3 years. Despite their directly benefiting from the SEF (the fishery infrastructure is State-based), most State governments view funding SEF research as a federal responsibility. SETMAC and AFMA have demonstrated a continuing commitment to scientific monitoring by contracting the ISMP for the 5-year period 2000–04.

The current emphasis on single-species stock assessment continues to over-ride the need for more strategic, holistic research, given the comparatively limited resources available. The SEF is a complex, multi-species fishery spanning many habitat types and located in an area where warm East Australian Current waters and colder, nutrient-rich sub-Antarctic waters interface. Many localized fisheries are highly seasonal (Klaer and Tilzey 1994). Little is known of the ways in which oceanographic cycles influence fish production, movement and catchability, nor of the mechanisms that drive fish recruitment. As mentioned previously, non-quota species are currently accorded little research attention. Studies such as the SEF Ecosystem Study recently completed by CSIRO (Bax and Williams 2000) are attempting to understand the fundamental, under-lying dynamics of the fishery. Increasingly important conservation issues, such as the effects of fishing on non-target fish species and the environment, also need to be addressed, particularly since the *Environment Protection and Biodiversity Conservation Act 1999* came into force.

Over the past two decades, considerable progress has been made towards providing SEF managers with a firmer scientific basis for decision making. However, from a scientific perspective, we are still a long way from adequately understanding the fishery. For example, the stock structure and basic life history of many quota species are still unknown. Whereas research aimed at developing management tools to cope with uncertainty is increasing, research on the factors underlying this uncertainty lacks adequate resources. In general, assessment scientists are frustrated by the failure of managers to apply the precautionary principle, despite the fact that biomass estimates for major species such as gemfish and orange roughy have fallen well below the biological reference points adopted by management as minimum desirable stock sizes.

From 1992 to 1999, trawl TACs for 13 of the 17 quota species have either remained at their original levels, which were mostly derived from historic annual catch maxima, or have increased. For example, the original TAC of 3000 t for the flathead species group was based on a sustainable yield estimate of 2500 t per annum for the main species, tiger flathead (Rowling 1994). However, by 1999 the allocated TAC had risen to 3966 t, and 1999 flathead landings totalled 3561 t. SEFAG's review in 2000 of the management implications of this level of catch concluded that 'estimates of fishing mortality are high; the current TAC is above previous estimates of long term sustainable yield, and above levels that have previously led to overfishing'. Despite this advice, the TAC allocated for 2001 remained high (3518 t).

Between 1992 and 1999 SEF trawl fishing effort (hours bottom time) increased by 75% but landings of many quota species declined. The most notable declines occurred off NSW where the modern trawl fleet has been operating for the longest time. Very significant declines have also been observed for some non-quota species in this area (Graham *et al.* 2001). Clearly, socio-economic management objectives (Grieve and Richardson 2001) continue to over-ride concerns about resource sustainability – e.g. the allocation of relatively large 'by-catch' TACs for eastern gemfish in the years from 1998 to 2000, despite indications of further declines in mature biomass and pleas for a more precautionary approach (Rowling 1998). Good science does not translate into good management without the political will to act on scientific findings

Acknowledgments

We thank all our scientific colleagues associated with the SEF who freely supplied information and Albert Caton and three anonymous referees who provided valuable input into revision of the manuscript.

References

Abel, K., Williams, M., and Smith, P. (Eds) (1991). Australian and New Zealand Southern Trawl Conference: Issues and Opportunities. Bureau of Rural Resources Proceedings No. 10. (BRS and ABARE: Canberra.)

Allen, K. R. (1989). A cohort analysis of the gemfish stock of south-east Australia. Report prepared on behalf of Unisearch Ltd for the Fishing Industry Research and Development Council, August 1989. (Department of Primary Industry and Energy: Canberra). 51 pp.

Andrew, N. L., Graham, K. J., Hodgson, K. E., and Gordon, G. N. G. (1997). Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. Final Report to FRDC. Project No. 96/139.

Anon. (1978). Economic survey – east coast trawl and Danish seine fishery 1972/3, 1973/4 and 1974/5 – preliminary report. (Fisheries Division, Department Primary Industry: Canberra.)

Anon. (1989). Management of the South East Trawl Fishery: a report of an Australian Fisheries Council Sub-Committee. (Department Primary Industry and Energy: Canberra.) 70 pp.

Baelde, P. (1991). Assessment of the Australian deep-water royal red prawn stock using commercial catch and effort data. *Fisheries Research* **12**, 243–58.

Baelde, P. (1992). Reproductive biology of commercially exploited deep-water royal red prawns (*Haliporoides sibogae*, Solenoceridae), Australia. *Marine Biology* **113**, 447–56.

Baelde, P. (1994). Growth, mortality and yield-per-recruit of deep-water royal red prawns (*Haliporoides sibogae*) off eastern Australia, using the length-based MULTIFAN method. *Marine Biology* **118**, 617–25.

Baelde, P. (1995). Analysis of the blue-eye trevalla fishery off Tasmania. In 'Assessment of the Blue-eye Trevalla Fishery and Analysis of the Impact of Mid-water Trawling'. Final Report to FRDC. Project No. 91/20.

Baelde, P. (1996). Biology and dynamics of the reproduction of blue eye trevalla, *Hyperoglyphe antarctica* (Centrolophidae), off Tasmania, southern Australia. *Fishery Bulletin (US)* **94**, 199–211.

Barker, B., Helmond, I., Bax, N., Williams, A., Davenport, S., and Wadley, V. (1999). A vessel-towed camera platform for sea-floor surveys of the continental shelf. *Continental Shelf Research* **19**, 1161–70.

Baulch, K., and Pascoe, S. (1992). Bycatch management options in the south east fishery. ABARE Research Report 92, 18. 42 pp.

Bax, N. J. (1997). The potential for spatial management and mesh size restriction for reducing bycatch of undersized tiger flathead off southeast Australia. Fisheries Bycatch. Alaska Sea Grant Report 97/02, 87–90.

Bax, N. J., and Williams, A. (Eds) (2000). Habitat and fisheries production in the South East Fishery. Final report to FRDC. Project 94/040.

Bax, N. J., and Williams, A. (2001). Seabed habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring. *Marine and Freshwater Research* **52**, 491–512.

Bax, N., Williams, A., Davenport S., and Bulman, C. (1999*a*). Managing the ecosystem by leverage points: a model for a multispecies fishery. Ecosystem Approaches for Fisheries Management. Alaska Sea Grant College Program AK-SG-99-01, 1–21.

Bax, N. J., Kloser, R., Williams, A., Gowlett-Holmes, K., and Ryan, T. (1999*b*). Seafloor habitat definition for spatial management in fisheries: a case study on the continental shelf of south-east Australia using acoustics and biotic assemblages. *Acta Oceanologica* **22**, 707–19.

Bax, N., Williams, A., and Althaus, F. (1999*c*). Development of a rapid-assessment technique to determine biological interactions of fish, their environment, and ecosystem functioning. Final report to FRDC. Project 96/275.

Bax, N. J., Burford, M., Clementson, L., and Davenport, S. (2001). Phytoplankton blooms and production sources on the south-east Australian continental shelf. *Marine and Freshwater Research* **52**, 451–62.

Bell J. D., Lyle J. M., Bulman C. M., Graham K. J., Newton G. M., and Smith D. C. (1992). Spatial variation in reproduction, and occurrence of non-reproductive adults, in orange roughy, *Hoplostethus atlanticus* Collett (Trachichthyidae), from south-eastern Australia. *Journal of Fish Biology* **40**, 107–22.

Beverton, R. J. H., and Holt, S. J. (1957). On the dynamics of exploited fish populations. Fishery Investigations Series 2 (London) No. 19.

Blaber, S. J. M. (1984). CSIRO's southern deepwater study begins. *Australian Fisheries* **43**, 15.

Blackburn, M. (1949). The barracouta *Thyrsites atun* (Euphrasen) in Australian waters: preliminary notes on the biology, and condition and future of the fishery. CSIRO (Australia) Report No. 93.

Blackburn, M. (1950). The condition of the fishery for barracouta *Thyrsites atun* (Euphrasen) in Australian waters. *Australian Journal of Marine and Freshwater Research* **1**, 110–28.

Blackburn, M. (1957). The relation between the food of the Australian barracouta *Thyrsites atun* (Euphrasen) and recent fluctuations in the fisheries. *Australian Journal of Marine and Freshwater Research* **8**, 29–54.

Blackburn, M. (1960). A study of condition (weight for length) of Australian barracouta *Thyrsites atun* (Euphrasen). *Australian Journal of Marine and Freshwater Research* **11**, 11–41.

Blackburn, M. (1978). Changes in size composition, indicative of stock conditions in the New South Wales trawl fishery, from 1945/46 to 1966/67. Australian CSIRO Division of Fisheries and Oceanography, Report No. 97, 76 pp.

Blackburn, M. (1979). The gemfish *Rexea solandri* (Cuvier and Valenciennes): distribution and length data from Australian east coast shelf waters. CSIRO Division Fisheries and Oceanography, Report No. 103, 11 pp.

Blackburn, M., and Gartner, P. E. (1954). Populations of barracouta *Thyrsites atun* (Euphrasen) in Australian waters. *Australian Journal of Marine and Freshwater Research* **5**, 411–68.

Bolch, C J. S., Elliot, N. G., and Ward, R. D. (1993). Enzyme variation in south-eastern Australian samples of the blue-eye or deepsea trevalla, *Hyperoglyphe antarctica* Carmichael 1818 (Teleostei: Stromateoidei). *Australian Journal of Marine and Freshwater Research* **44**, 687–98.

Bolch, C. J. S., Ward, R. D., and Last, P. R. (1994). Biochemical systematics of the marine fish family Centrolophidae (Teleostei : Stromateoidea) from Australian waters. *Australian Journal of Marine and Freshwater Research* **45**, 1157–72.

Brown, D. (1997). Australian Fisheries Surveys Report 1997. (ABARE: Canberra.)

Bruce, B. D. (1988). Larval development of blue grenadier, *Macruronus novaezelandiae* (Hector), in Tasmanian waters. *Fishery Bulletin (US)* **86**,119–28.

Bruce, B. D., Young, J. W., Evans, K., Sutton, C. A., and Furlani, D. M. (in press). The influence of mesoscale physical oceanographic processes on larval distribution and stock structure in jackass morwong (*Nemadactylus macropterus*). *ICES Journal of Marine Science*

Bruce, B. D., Neira, F. J., and Bradford, R. W. (2001*a*). Larval distribution and abundance of blue and spotted warehous (*Seriolella brama* and *S. punctata* : Centrolophidae) in south-eastern Australia. *Marine and Freshwater Research* **52**, 631–6.

Bruce, B. D., Condie, S. A., and Sutton, C. A. (2001*b*). Larval distribution of blue grenadier (*Macruronus novaezelandiae* Hector) in south-eastern Australia: further evidence for a second spawning area. *Marine and Freshwater Research* **52**, 603–10.

Bulman, C. M., and Blaber, S. J. M. (1986). Feeding ecology of *Macruronus novaezelandiae* (Hector) (Teleostei : Merlucciidae) in south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **37**, 621–39.

Bulman, C. M., and Koslow, J. A. (1992). Diet and food consumption of a deep-sea fish, orange roughy *Hoplostethus atlanticus* (Pisces : Trachichthyidae), off southeastern Australia. *Marine Ecology Progress Series* **82**, 115–29.

Bulman, C. M., and Koslow, J. A. (1995). Development and depth distribution of the eggs of orange roughy, *Hoplostethus atlanticus* (Pisces : Trachichthyidae). *Marine and Freshwater Research* **46**, 697–705.

Bulman, C. M., Koslow, J. A., and Haskard, K. A. (1999). Estimation of the spawning stock biomass of blue grenadier (*Macruronus novaezelandiae*) off western Tasmania based upon the annual egg production method. *Marine and Freshwater Research* **50**, 197–207.

Bulman, C., Althaus, F., He, X., Bax, N. J., and Williams, A. (2001). Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine and Freshwater Research* **52**, 537–48.

Chesson, J. (Ed.) (1996). The South East Fishery 1995. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Chesson, J. (Ed.) (1997). The South East Fishery 1996. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Colefax, A. N. (1934). A preliminary investigation of the natural history of the tiger flathead (*Neoplatycephalus macrodon*) on the south-eastern Australian coast. I. Distribution and supply, length statistics. *Proceedings of the Linnaean Society of NSW* **59**, 71–91.

Colefax, A. N. (1938). A preliminary investigation of the natural history of the tiger flathead (*Neoplatycephalus macrodon*) on the south-eastern Australian coast. II. *Proceedings of the Linnaean Society of NSW* **63**, 155–64.

Colgan, D. J., and Paxton, J. R. (1997). Biochemical genetics and recognition of a western stock of the common gemfish, *Rexea solandri* (Scombroidea:Gempylidae), in Australia. *Marine and Freshwater Research* **48**, 103–18.

Collins, S. P., and Baron, M. P. (1981). Demersal and pelagic trawling survey of the MT *Denebola* in southern Australian waters, 1979–1980 summer. *Tasmanian Fisheries Research* **24**, 2–48.

Dakin, W. J. (1939). The age determination of the tiger flathead *Neoplatycephalus macrodon* (Ogilby) by means of otoliths. *Records of the Australian Museum* **20**, 282–92.

Daley, R. K., Last, P. R., Yearsley, G. K., and Ward, R. D. (1997). South East fishery quota species – an identification guide. (CSIRO Marine Research: Hobart, Australia.) 91 pp.

Daley, R. K., Last, P. R., and Ward, R. W. (1998). Resolution of taxonomic problems and preparation of a user friendly guide to whole fish and fillets for the quota species of the south east fishery. Final report: Fishing Industry Research and Development Trust Fund Project 92–3/22, pp. 1–27. (CSIRO Division of Fisheries: Hobart, Australia.)

Dannevig, H. C. (1913). Fisheries. Notes on Australian fisheries with a summary of the results obtained by the FIS *Endeavour*. (Commonwealth Department of Trade and Customs: Canberra.)

Diplock, J. H. (1984). A synopsis of available data on redfish *Centroberyx affinis* from NSW waters. In 'Proceedings of the Demersal and Pelagic Fish Research Group workshop on trawl fish resources, Sydney, March 27–29, 1984'. (South Eastern Fisheries Committee, DPI: Canberra.)

DPIE (1989). New directions for Commonwealth fisheries management in the 1990s. (Australian Government Publishing Service: Canberra.) 114 pp.

Elliott, N. G., and Kloser, R. J. (1993). Use of acoustics to assess a small aggregation of orange roughy, *Hoplostethus atlanticus* (Collett), off the eastern coast of Tasmania. *Australian Journal of Marine and Freshwater Research* **44**, 473–82.

Elliott, N. G., and Ward, R. D. (1992). Enzyme variation in orange roughy, *Hoplostethus atlanticus* (Teleostei : Trachichthyidae), from southern Australian and New Zealand waters. *Australian Journal of Marine and Freshwater Research* **43**, 1561–71.

Elliott N. G., Haskard K. A., and Koslow J. A. (1995). Morphometric analysis of orange roughy (*Hoplostethus atlanticus*) off the continental slope of southern Australia. *Journal of Fish Biology* **46**, 202–20

Elliott N. G., Lowry P. S., Grewe P. M., Innes B. H., Yearsley G. K., and Ward R. D. (1998). Genetic evidence for Departmenth- and spatially separated stocks of the deep-water spikey oreo in Australasian waters. *Journal of Fish Biology* **52**, 796–816.

Evans, K. (1986). Length/frequency, age and mortality estimates of blue grenadier, generated from 1984 commercial catch data. In 'Workshop on Trawl Fish Resources, Working Papers, Queenscliff, 2–3 May 1986, Vol. 1'. pp. 1–5. (DPFRG, South Eastern Fisheries Committee, DPI: Canberra.)

Fairbridge, W. S. (1948). The effect of the war on the eastern Australian trawl fishery. *Journal of the Council of Science and Industrial Research* **21**, 75–98.

Fairbridge, W. S. (1950). Third warning on overfishing of trawling grounds. *Fisheries Newsletter* **9**(1), 9.

Fairbridge, W. S. (1951*a*). The overfishing of the east Australian trawl fishery. Indo-Pacific Fisheries Council Proceedings No. 2, 73–9.

Fairbridge, W. S. (1951*b*). The New South Wales tiger flathead, *Neoplatycephalus macrodon* (Ogilby). I. Biology and age determination. *Australian Journal of Marine and Freshwater Research* **2**, 117–78.

Fairbridge, W. S. (1952*a*). The New South Wales tiger flathead, *Neoplatycephalus macrodon* (Ogilby). II. The age composition of the commercial catch, overfishing of the stocks, and suggested conservation. *Australian Journal of Marine and Freshwater Research* **3**, 1–31.

Fairbridge, W. S. (1952*b*). Condition of trawl fishery worsens. *Fisheries Newsletter* **11**(10), 13.

Ford, W., and Lyle, J. (1992). Catalogue and analysis of historic catch, effort and biological data for the South East Trawl fishery. Final Report to FRDC (Part A). Project no. 90/23.

Graham, K. J., Winstanley, R. H., and Wilson, M. A. (1982). Fishery Situation Report No. 9: Trawl and Danish seine fishery. (South Eastern Fisheries Committee, CSIRO Marine Laboratories: Cronulla, Australia.)

Graham, K. J., Andrew, N. L., and Hodgson, K. E. (2001). Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research* **52**, 549–61.

Grant, C. J., Cowper, T. R., and Reid, D. D. (1978). Age and growth of snoek, *Leionura atun* (Euphrasen) in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **29**, 435–44.

Grieve, C., and Richardson, G. (2001). Recent history of Australia's South East Fishery: a manager's perspective. *Marine and Freshwater Research* **52**, 377–86.

Gunn, J. S., Bruce, B. D., Furlani, D. M., Thresher, R. E., and Blaber, S. J. M. (1989). Timing and location of spawning of blue grenadier, *Macruronus novaezelandiae* (Teleostei : Merlucciidae) in Australian coastal waters. *Australian Journal of Marine and Freshwater Research* **40**, 97–112.

Harrison, A. J. (1991). The Commonwealth Government in the administration of Australian fisheries: a sort of mongrel socialism. RAIPA National Monograph No. 6. 96pp.

Hogan, L., Thorpe, S., and Timcke, D. (1999). Tradable quotas in fisheries management: implications for Australia's South East Fishery. Report to the Fisheries Resources Research Fund. (ABARE: Canberra.)

Houston, T. W. (1955). The New South Wales trawl fishery: review of past course and examination of present condition. *Australian Journal of Marine and Freshwater Research* **6**, 165–208.

Jarzynski, S. (1980). The New South Wales Trawl and Danish Seine Fishery – a report of an economic survey 1975/6 to 1977/8. (Fisheries Division, Department Primary Industry: Canberra.)

Jordan, A. J. (1997). Demersal trawl surveys of the continental shelf of southern and south-eastern Tasmania 1993–95. Technical Report No 50 (Marine Research Laboratories, Department of Primary Industry and Fisheries: Tasmania.) 148 pp.

Jordan, A. R. (2001*a*). Spatial and temporal variations in abundance and distribution of juvenile and adult jackass morwong, *Nemadactylus macropterus*, in south-eastern Tasmania. *Marine and Freshwater Research* **52**, 661–70.

Jordan, A. R. (2001*b*). Age, growth and spatial and interannual trends in age composition of jackass morwong, *Nemadactylus macropterus*, in Tasmania. *Marine and Freshwater Research* **52**, 651–60.

Jordan, A. R. (2001*c*). Reproductive biology, early life-history and settlement distribution of sand flathead (*Platycephalus bassensis*) in Tasmania. *Marine and Freshwater Research* **52**, 589–601.

Kenchington, T. J. (1989). Estimation of catchability coefficients. *Marine Biology* **101**, 24–5.

Kenchington, T. J., and Augustine, O. (1987). Age and growth of blue grenadier, *Macruronus novaezelandiae* (Hector), in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **38**, 625–46.

Klaer, N. L. (2001). Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. *Marine and Freshwater Research* **52**, 399–410.

Klaer, N. L., and Tilzey, R. D. J. (1994). The multi-species structure of the fishery. In 'The South East Fishery: a Scientific Review with Reference to Quota Management'. (Ed. R. D. J. Tilzey.) pp. 72–94. (Australian Government Publishing Service: Canberra.)

Klaer, N. L., and Tilzey, R. D. J. (1996). Catalogue and analysis of historic catch, effort and biological data for the South East trawl fishery. Final Report to FRDC (Part B). Project no. 90/23.

Kloser, R. J. (1996). Improved precision of acoustic surveys of benthopelagic fish by means of a deep-towed transducer. *ICES Journal of Marine Science* **53**, 407–13.

Kloser, R. J., Koslow, J. A., and Williams, A. (1996). Acoustic assessment of the biomass of a spawning aggregation of orange roughy (*Hoplostethus atlanticus*, Collett) off south-eastern Australia, 1990–93. *Marine and Freshwater Research* **47**, 1015–24.

Kloser, R. J., Williams, A., and Koslow, J. A. (1997). Problems with acoustic target strength measurements of a deepwater fish, orange roughy (*Hoplostethus atlanticus*, Collett). *ICES Journal of Marine Science* **54**, 60–71.

Kloser, R. J., Bax, N. J., Ryan, T., Williams, A., and Barker, B. A. (2001). Remote sensing of seabed types in the Australian South East Fishery; development and application of normal incident acoustic techniques and associated 'ground truthing'. *Marine and Freshwater Research* **52**, 475–89.

Knuckey, I. A., and Sivakumaran, K. P. (1999). Spawning and reproductive characteristics of blue warehou in south-east Australia waters. Final Report to FRDC. Project 96/142. 49 pp. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Knuckey, I. A., and Sivakumaran, K. P. (2001). Reproductive characteristics and per-recruit analyses of blue warehou (*Seriolella brama*): implications for the South East Fishery of Australia. *Marine and Freshwater Research* **52**, 575–87.

Knuckey, I. A., and Smith, D. C. (1997). Pilot egg survey of orange roughy in the South East Fishery's Western Zone. Final Report to FRDC. Project 96/110. 22 pp. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Knuckey, I. A., MacDonald, C. M., Lyle, J. M., and Smith, D. C. (1999). Movement and exploitation rates of blue and spotted warehou – a pilot tagging study. Final Report to FRDC. Project 94/023. 49 pp. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Knuckey, I. A., Grieve, C., and Smith, D. C. (in press). Evolution of the integrated scientific monitoring programme in Australia's South East Fishery. In 'Proceedings of the International Conference on Integrated Fisheries Monitoring'. 2–5 January 1999, Sydney.

Koslow, J. A. (1996). Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *Journal of Fish Biology* **49**(Suppl. A) 54–74.

Koslow, J. A., and Gowlett-Holmes, K. (1998). The seamount fauna of southern Tasmania: impacts of trawling and its conservation. Report to Environment Australia and FRDC (Project no. 95/058.)

Koslow, J. A., Bulman, C. M., and Lyle, J. M. (1994*a*). The mid-slope demersal fish community off southeastern Australia. *Deep-Sea Research* **41**, 113–41.

Koslow, J. A., Kloser, R., and Williams, A. (1994*b*). Development and use of acoustic techniques for the assessment of deepwater commercial fish stocks. Final Report to FRDC. Project no. 93/237. 131 pp.

Koslow, J. A., Bulman, C. M., Lyle, J. M., and Haskard, K. A. (1995*a*). Biomass assessment of a deep-water fish, the orange roughy (*Hoplostethus atlanticus*), based on an egg survey. *Marine and Freshwater Research* **46**, 819–30.

Koslow, J. A., Bell, J., Virtue, P., and Smith, D. C. (1995*b*). Fecundity and its variability in orange roughy (*Hoplostethus atlanticus*): effects of population density, condition, egg size and senescence. *Journal of Fish Biology* **47**, 1063–80.

Koslow, J. A., Kloser, R. J., and Stanley, C. A. (1995*c*). Avoidance of a camera system by a deepwater fish, the orange roughy (*Hoplostethus atlanticus*) *Deep-Sea Research* I **42**, 233–44.

Koslow, J. A., Kloser, R. J., and Williams, A. (1997). Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. *Marine Ecology Progress Series* **146**, 21–35.

Larcombe, J. W. P., McLoughlin, K. J., and Tilzey, R. D. J. (2001). Trawl operations in the South East Fishery, Australia: spatial distribution and intensity. *Marine and Freshwater Research* **52**, 419–30.

Last, P. R., and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' (CSIRO Publishing: Melbourne.) 601 pp.

Last, P. R., Scott, E. O. G., and Talbot, F. H. (1983). 'Fishes of Tasmania.' (Tasmanian Fisheries Development Authority: Hobart.) 563 pp.

Liggins, G. W. (1996). The interaction between fish trawling in NSW and other commercial and recreational fisheries. Final Report to FRDC. Project 92/79.

Lorimer, P. D., and Barker, D. J. (1967). The east coast trawl fishery. Proceedings Australian Fisheries Development Conference, Canberra, February 20–22, 1967. (Department Primary Industry: Canberra.)

Lyle, J. M., Kitchener, J. A., and Riley, S. P. (1991). An assessment of the orange roughy resource off the coast of Tasmania. Final report to FRDC. Project 87/65, 129 pp.

May, J. L., and Blaber, S. J. M. (1989). Benthic and pelagic fish biomass of the upper continental slope off eastern Tasmania. *Marine Biology* **101**, 11–25.

Menz, K., Geen, G., and Collins, D. (1986). Issues in the management of the South-East Trawl Fishery. Bureau of Agricultural Economics Discussion Paper No. 86. 2. (Australian Government Publishing Service: Canberra.)

Milton, D. A., and Shaklee, J. B. (1987). Biochemical genetics and population structure of blue grenadier, *Macruronus novaezelandiae* (Hector) (Pisces : Merlucciidae), from Australian waters. *Australian Journal of Marine and Freshwater Research* **38**, 727–42.

Montgomery, S. S. (1985). Aspects of the biology of the tiger flathead *Platycephalus richardsoni* and the associated fishery. MSc Thesis, University of New South Wales, Australia.

Morison, A. K. (1996). Age and growth of major species in the South East Fishery. Marine and Freshwater Resources Institute Report. pp. 18. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Morison, A. K., Robertson, S. G., and Smith, D. C. (1998). An integrated system for production fish ageing: image analysis and quality assurance. *North American Journal of Fisheries Management* **18**, 587–98.

Morison, A. K., Green, C. P., and Smith, D. C. (1999). Estimation of mortality of ling based on historical length and otolith collections from the eastern sector of the South East Fishery. Final Report to FRDC Project No. 95/96–10. 22 pp. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Nicoll, R. (1993*a*). A breakthrough in Bendigo. *Australian Fisheries* **52**(1), 6–9.

Nicoll, R. (1993*b*). Geelong brings a resolve to make workshops better. *Australian Fisheries* **52**(12), 6–10.

Park, T. J. (1994). Ocean perch, *Helicolenus* sp. In 'The South East Fishery: a Scientific Review with Reference to Quota Management'. (Ed. R. D. J. Tilzey.) pp. 237–46. (Australian Government Publishing Service: Canberra.)

Parslow, J. S., Koslow, J. A., Griffiths, F. B., Clementson, L., Rathbone, C., Bonham, P., and McKenzie, D. (1996). Tasmanian slope trophodynamics: final report. (CSIRO Division of Fisheries: Hobart, Australia.)

Paxton, J. R., and Colgan, D. J. (1993). Biochemical genetics and stock assessment of common gemfish and ocean perch. Final Report to FRDC. Project No. 91/35.

Prince, J., Baelde, P., and Wright, G. (1998). Synthesis of industry information on fishing patterns, technological change and the influence of oceanographic effects on SEF fish stocks. Final Report to FRDC. Project no. 97/114.

Punt, A. E., and Smith, A. D. M. (1999*a*). Management of long-lived marine resources: a comparison of feedback-control management procedures. In 'Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals'. (Ed. J. A. Musick.) pp. 243–65. American Fisheries Society Symposium 23, Bethesda, MD.

Punt, A. E., and Smith, A. D. M. (1999*b*). Harvest strategy evaluation for the eastern stock of gemfish (*Rexea solandri*). *ICES Journal of Marine Science* **56**, 860–75.

Ross, D. M., and Smith, D. C. (1997). The Australian orange roughy fishery: a process for better resource management. In 'Developing and Sustaining World Fisheries Resources: the State of Science and Management'. 2nd World Fisheries Conference Proceedings. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. P. Beumer.) pp. 256–60. (CSIRO Publishing: Melbourne.)

Roughley, T. C. (1951). 'Fish and Fisheries of Australia.' (Angus and Robertson: Sydney.)

Rowling, K. R. (1979). NSW trawl fish study highlights importance of deepwater catches. *Australian Fisheries* **38**(4), 9–14.

Rowling, K. R. (1987). The need for catch controls in the gemfish fishery. NSW Department of Agriculture, Fisheries Research Institute Internal Report No. 26.

Rowling, K. R. (1990*a*). Changes in the stock composition and abundance of spawning gemfish *Rexea solandri* (Cuvier), Gempylidae, in south eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **41**, 145–63.

Rowling, K. R. (1990*b*). Estimation of fishing mortality, stock unity and growth of redfish *Centroberyx affinis* by tagging. Final report to FIRTA. Project 85/71. (NSW Department Agriculture and Fisheries, Fisheries Research Institute: Cronulla, Australia.)

Rowling, K. R. (1994). Tiger flathead, *Neoplatycephalus richardsoni*. In 'The South East Fishery: a Scientific Review with Reference to Quota Management'. (Ed. R. D. J. Tilzey.) pp. 124–36. (Australian Government Publishing Service: Canberra.)

Rowling, K. R. (1996). Assessment of the NSW dropline fishery: progress report, 1993 to 1995. (NSW Fisheries Research Institute: Cronulla, Australia.) 37 pp.

Rowling, K. R. (1997). The collapse of the eastern Australian gemfish stock - issues for management and the role of fisheries science. In 'Developing and Sustaining World Fisheries Resources: the State of Science and Management'. 2nd World Fisheries Conference Proceedings. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. P. Beumer.) pp. 210–14. (CSIRO Publishing: Melbourne.)

Rowling, K. R. (1998). Eastern gemfish – is it time for a precautionary management approach? Background paper, 12th meeting of the Eastern Gemfish Assessment Group, 1–2 October, 1988. (Australian Fisheries Management Authority: Canberra.) 8 pp.

Rowling, K. R. (1999). Biological and fishery data available from study of the New South Wales deepwater dropline fishery. (NSW Fisheries Research Institute: Cronulla, Australia.) 24 pp.

Rowling, K. R. (2001). Redfish, 1999. Stock Assessment Report. South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Rowling, K. R., and Raines, L. P. (2000). Description of the biology and an assessment of the fishery for silver trevally *Pseudocaranx dentex* off New South Wales. Final Report to FRDC. Project No. 97/125.

Rowling, K. R., and Reid, D. D. (1992). Effect of temporal changes in size composition on estimates of von Bertalanffy growth parameters for gemfish, *Rexea solandri* (Cuvier), Gempylidae. *Australian Journal of Marine and Freshwater Research* **43**, 1229–39.

Sainsbury, K. J. (1988). The ecological basis of multi-species fisheries, and management of a demersal fishery in tropical Australia. In 'Fish Population Dynamics'. (Ed. J. A. Gulland.) pp. 349–82. (Wiley: Chichester.)

Smith, A. D. M., and Punt, A. E. (1998). Stock assessment of gemfish (*Rexea solandri*) in eastern Australia using maximum likelihood and Bayesian methods. In 'Fisheries Stock Assessment Models'. (Eds T. J. Quinn II, F. Funk, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan and C-I Zhang.) pp. 245–86. Alaska Sea Grant College Program, AK-SG-98-01.

Smith, A. D. M., Sainsbury, K. J., and Stevens, R. A. (1999). Implementing effective fisheries-management systems – management strategy evaluation and the Australian partnership approach. *ICES Journal of Marine Science* **56**, 967–79.

Smith, D. C. (1982). Age and growth of jackass morwong (*Nemadactylus macropterus* Bloch and Schneider) in eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **33**, 245–53.

Smith, D. C. (1983). Annual total mortality and population structure of jackass morwong (*Nemadactylus macropterus* Bloch and Schneider) in eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **34**, 253–60.

Smith, D. C., and Stewart, B. D. (1994). Development of methods to age commercially important dories and oreos. Final Report to FRDC. Project no. 91/036.

Smith, D. C., McCoy, P., and Cottier, J. (1994). Assessment of the trawl and gillnet fisheries for the warehous. Final Report to FRDC. Project no. 90/011.

Smith, D. C., Huber, D., Woolcock, J., Withell, A., and Williams, S. (1995*a*). Western Bass Strait Trawl Fishery Assessment Program. Final Report to FRDC. Project no. 86/039.

Smith, D. C., Fenton, G. E., Robertson, S. G., and Short, S. A. (1995*b*). Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annuli counts with radiometric ageing. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 391–401.

Smith, D. C., Morison, A. K., and Robertson, A. K. (1996). The Age Composition of Ling Catches and Ling Stock Assessment Workshop. Final Report to FRDC. Project no. 94/148.

Smith, D. C., Gilbert, D. J., Gason, A., and Knuckey, I. A. (1997). Design of an integrated scientific monitoring program for the South East Fishery. Final Report to Australian Fisheries Management Authority. 50 pp. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Smith, D. C., Robertson, S. G., and Morison, A. K. (1998*a*). Age composition of orange roughy in the eastern and southern management zones. Final Report to FRDC Project no. 95/032.

Smith, P., Griffiths, G., and Ruello, N. (1998*b*). Price formation on the Sydney Fish Market. ABARE Research Report No. 98.8. (ABARE: Canberra.)

Staples, D., and Tilzey, R. (Eds) (1995). The South East Fishery 1994. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Staples, D., Smith, D., and Lyle, J. (Eds) (1994). The South East Fishery 1993. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Thresher, R. E., Bruce, B. D., Furlani, D. M., and Gunn, J. S. (1989). Distribution, advection and growth of larvae of the southern temperate gadoid, *Macruronus novaezelandiae* (Teleostei : Merlucciidae), in Australian coastal waters. *Fishery Bulletin (US)* **87**, 17–28.

Thresher, R. E., Proctor, C. H., Evans, K. J., and Mackinnon, C. J. (1999). Completion of an analysis of stock structure of orange roughy, based on otolith chemical composition. CSIRO Division of Marine Research. Final Report to FRDC 96/111. 51 pp.

Tilzey, R. D. J. (Ed.) (1994). 'The South East Fishery: a Scientific Review with Reference to Quota Management.' (Australian Government Publishing Service: Canberra.) 360 pp.

Tilzey, R. (Ed.) (1998). The South East Fishery 1997. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Tilzey, R. (Ed.) (1999). The South East Fishery 1998. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Tilzey, R. D. J., Zann-Schuster, M., Klaer, N. L., and Williams, M. E. (1990). The South East Trawl Fishery: biological synopses and catch distributions for seven major commercial fish species. Bureau of Rural Resources Bulletin No. 6. Australian Government Publishing Service: Canberra.)

Wankowski, J. W. J., and Moulton, P. L. (1986). Distribution, abundance and biomass estimates of commercially important demersal fish species in eastern Bass Strait, Australia. Victorian Department of Conservation Forests and Lands, Marine Science Technical Report No. 62. 57 pp.

Ward, R. W., and Last, P. R. (1993). Population structure of the blue-eye (deepsea trevalla), *Hyperoglyphe antarctica*. Final report: Fishing Industry Research and Development Trust Fund, Project 91/19, 69 pp. (CSIRO Division of Fisheries: Hobart, Australia.)

Ward, R. W., Elliott, N. G., Yearsley, G. K., and Last, P. R. (1996). Species and stock delineation of Australian oreos. Final report: Fishing Industry Research and Development Trust Fund, Project 92/24, 144 pp. (CSIRO Division of Fisheries: Hobart, Australia.)

Ward, R. D, Elliott, N. G., Grewe, P. M., Last, P. R., Lowry, P. S., Innes, B. H., and Yearsley, G. K. (1998). Allozyme and mitochondrial DNA variation in three species of oreos (Teleostei : Oreosomatidae) from Australasian waters. *New Zealand Journal of Marine and Freshwater Research* **32**, 233–45.

Williams, A., and Bax, N. J. (2001). Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52**, 513–36.

Williams, M. (1989). Orange roughy research in Australia: a case study for research co-ordination. *Search* **20**, 130–34.

Wilson, M. A. (1981). Blue grenadier spawning grounds. *FINTAS* **4**, 9–10.

Wilson, M. A. (1982*a*). Spawning blue grenadier caught off Cape Sorell. *FINTAS* **4**, 13.

Wilson, M. A. (1982*b*). Challenger reveals potentially important roughy resource off Tasmania. *Australian Fisheries* **41**(5), 2–3.

Wilson, M. A. (1984). An assessment of the lightly exploited trawl fish resources of the developing zone. DPFRG Workshop on Trawl Fish resources. Working Papers. Sydney 27–29 March, 1984, 265–87.

Yearsley, G. K., Last, P. R., and Ward, R. D. (1999). 'Handbook of Australian Seafood.' (CSIRO Marine Research: Hobart, Australia.) 461 pp.

Young, J. W., and Blaber, S. J. M. (1986). Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. *Marine Biology* **93**, 147–56.

Young, J. W., Blaber, S. J. M., and Rose, R. (1987). Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. *Marine Biology* **95**, 323–32.

Manuscript received 15 December 1999; revised 15 September 2000 and 2 February 2001; accepted 2 February 2001

Mar. Freshwater Res., 2001, **52**, 377–86

Recent history of Australia's South East Fishery; a manager's perspective

Chris Grieve[A] *and Geoff Richardson*[B]

[A]Institute for European Environmental Policy, 52 Horseferry Road, London SW1P 2AG, England.
email: cgrieve@ieeplondon.org.uk
[B]Australian Fisheries Management Authority, Box 7051, Canberra Mail Centre, ACT, 2610, Australia

Abstract. A brief history of the South East Fishery is presented, focussing on the period 1986–2000. With the realization in the 1980s that natural resources are finite, active fisheries management became more of a focus for the Australian Federal Government. This paper describes the Federal Government's fisheries management objectives since the mid 1980s as well as major new policy initiatives, and seeks to measure the performance of the fishery against key management objectives. A few simple indicators of change are examined with particular reference to the pursuit of economic efficiency.

Introduction

Fisheries management philosophy and objectives have evolved significantly over the past century and Australia's South East Fishery has been subjected to many of the emerging philosophies. Ample literature describes the origins and history of Australia's oldest trawl fishery (Smith 1991; Tilzey 1994). Smith (1991) and Tilzey (1994) summarize the major changes in the South East Fishery (SEF) from 1883 when exploratory beam trawling was attempted off the New South Wales (NSW) coast through to the introduction of individual transferable quotas (ITQs) in 1992. The present paper attempts to measure the most significant milestones in recent SEF management against the management objectives or philosophies of the day.

The SEF is a complicated fishery, now characterized by a wide geographical area, multiple species and multiple methods, operating in a variety of habitats from shallow coastal waters to depths of >1000 m with >100 species of fish and invertebrates sold commercially (Tilzey 1994).

Although it began as a trawl fishery, the SEF is no longer just that but two distinct method-based sectors that are edging towards the same management regime. It now includes the traditional and older South East Trawl Fishery (otter-board trawl, mid-water trawl and Danish seine) and the younger South East Non-trawl Fishery, called Non-trawl because it is a convenient description of the trap, line, seine- and mesh-net methods used to catch some of the same species of demersal scalefish as those trawled in the south-eastern region of Australia's Exclusive Economic Zone (Fig. 1)

The first 80 years

As reflected in the aphorism 'there are plenty more fish in the sea', in the community outside the world of the biologist the bounty of the oceans was thought to be limitless. In Australia in the first three-quarters of the twentieth century, successive Federal governments encouraged development of fishing as a source of employment in the rural sector, despite the concern of some government biologists with regard to stock depletions. The NSW government imported three steam trawlers from the UK in 1915, built four more in 1920 and sold the fleet to private concerns in 1923 (Klaer 2001). A commercial fishery had begun.

The day-to-day management of the fishery was left to State governments for the first 80 or so years. By 1952 the Federal government had enacted the *Fisheries Act 1952 (Cwlth)* and the trawl fishery had expanded from Sydney southwards to other large coastal towns in NSW such as Ulladulla and Eden and into the Victorian ports of Lakes Entrance and San Remo (Smith 1991). The fleet expanded and contracted over the years and, as the fleet became dominated by Danish-seiners, steam trawlers were used less and less until the last one left the fishery in 1961 (Smith 1991). Despite the enactment of federal law in 1952, the States continued to manage the day-to-day operations of the fishery until 1985. Restrictions regarding the minimum mesh size for trawl-net codends were brought in by the NSW government in the 1950s to limit the catch of juvenile flathead, *Neoplatycephalus richardsoni* (Rowling 1994*b*) and later extended to the whole SEF. In the 1970s vessel length was limited to 32 m overall and in 1979 one vessel per State (i.e. 4 vessels in total) of between 32 and 45.7 m was allowed to fish in the trawl fishery (Anon. 1989*a*). In

10.1071/MF00070 1323-1650/01/040377

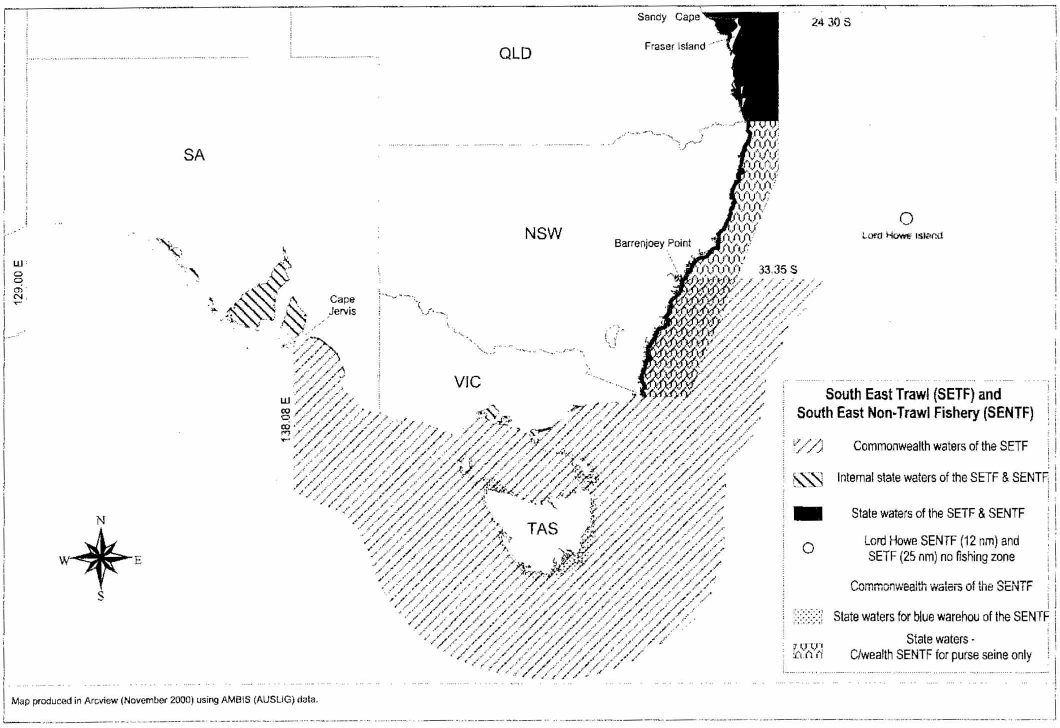


Fig. 1. Geographical boundaries of the trawl and non-trawl sectors of the South East Fishery, Australia.

effect, management of the fishery for the first three-quarters of the century was by minimal interference and open access.

Federal action

In 1979 the *Fisheries Act 1952 (Cwlth)* was amended to include management objectives. These required the Minister to ensure 'that the living resources of the AFZ [Australian Fishing Zone] are not endangered by over-exploitation' and have regard to 'achieving the optimum utilisation of the living resources of the AFZ'. From *c.* 1980, by which time trawl fishing effort had expanded southwards and outwards into the deeper waters of the continental shelf and the upper waters of the continental slope (Smith 1991), concern started to grow about the increasing fleet size, the level of capital invested in the trawl fishery (Menz *et al.* 1986) and the apparent declining economic position of operators (Anon. 1989*a*). A task force consisting of State and Federal fisheries management agencies was convened in 1983 to determine the need for additional management intervention (Menz *et al.* 1986).

In 1985 the Federal government defined the area of the South East Trawl Fishery (Barrenjoey Point, NSW to Cape Jervis, South Australia – Fig. 1) and limited entry to the fishery (Anon. 1989*a*). Restrictions on vessel length and trawl net mesh size were retained. Three management areas were created (Eastern Sectors A and B, and the South Western Sector) and vessels were granted Federal fishing boat licences endorsed to fish in one or more of these regions. In October 1985 a scientific logbook was introduced and operators were required to complete shot-by-shot catch records. By the end of 1986, 151 vessels had recorded catches in the fishery, employing ~84 000 h of trawl effort (Table 1).

A boat-replacement policy with the aim of reducing fleet capacity over time and ultimately controlling fishing effort was implemented in 1986 (Anon. 1989*a*). This introduced units of capacity to the fishery, these being based on hull

Table 1. Number of vessels recording a catch and hours of trawl effort in the South East Trawl Fishery, Australia, 1986–98
Source: AFZIS database, AFMA

Year	No. of boats	No. of hours
1986	151	84 013
1987	144	76 334
1988	148	80 731
1989	147	80 393
1990	147	72 637
1991	138	84 466
1992	122	71 841
1993	119	81 661
1994	112	87 653
1995	102	94 915
1996	112	101 697
1997	109	108 990
1998	102	102 781

dimensions and main engine power; at the policy's introduction there were ~22 000 units. When operators replaced or upgraded a vessel they had to obtain additional units from another operator to cover any increased capacity in the vessel as well as enough to account for the forfeiture of a proportion of those units to the government (Anon. 1989*a*). By 1989 the number of units of capacity in the fishery had increased to 24 086, with 2233 of these units not attached to operating vessels (Anon. 1989*a*). Litigation that successfully challenged the application of the limited-entry policy was largely responsible for the increase instead of the expected decrease in units of capacity in the fishery.

The input control[1] regime came under increasing fishing pressure during the late 1980s as a result of two unrelated events in the fishery. At the same time as the eastern gemfish (*Rexea solandri*) began to show signs of recruitment failure (Rowling 1994*a*), large aggregations of orange roughy (*Hoplostethus atlanticus*) were discovered off southern and eastern Tasmania (Lyle 1994). This precipitated a shift of trawl licences and units from the traditional east-coast operators who typically used small vessels (<20 m length) to larger steel-hulled vessels working in the south-western sector (Geen *et al.* 1991; Lack 1991); The decrease in effort off the NSW coast and increase in the south and west of the fishery was evident by 1990 (Fig. 2).

It is widely acknowledged that the objectives of the input-control regime in the trawl fishery were not achieved (Anon. 1989*a*; Geen *et al.* 1991; Lack 1991; Tilzey 1994) and that management of the fishery had to change. The task force summarized the fishery (Anon. 1989*a*) as being characterized by

- a persistent and worsening economic situation while management continues to be based on control of inputs which relies on reducing economic efficiency;
- a number of species under severe biological stress.... while existing arrangements do not appear to be able to contain aggregate effort;
- the need for an increasing number of management measures; and
- a reliance on quantity of product rather than attempting to increase returns from smaller quantities by improving quality.

Before 1985, the non-trawl sector was a series of small, open-access fisheries. In July 1985, the issue of new

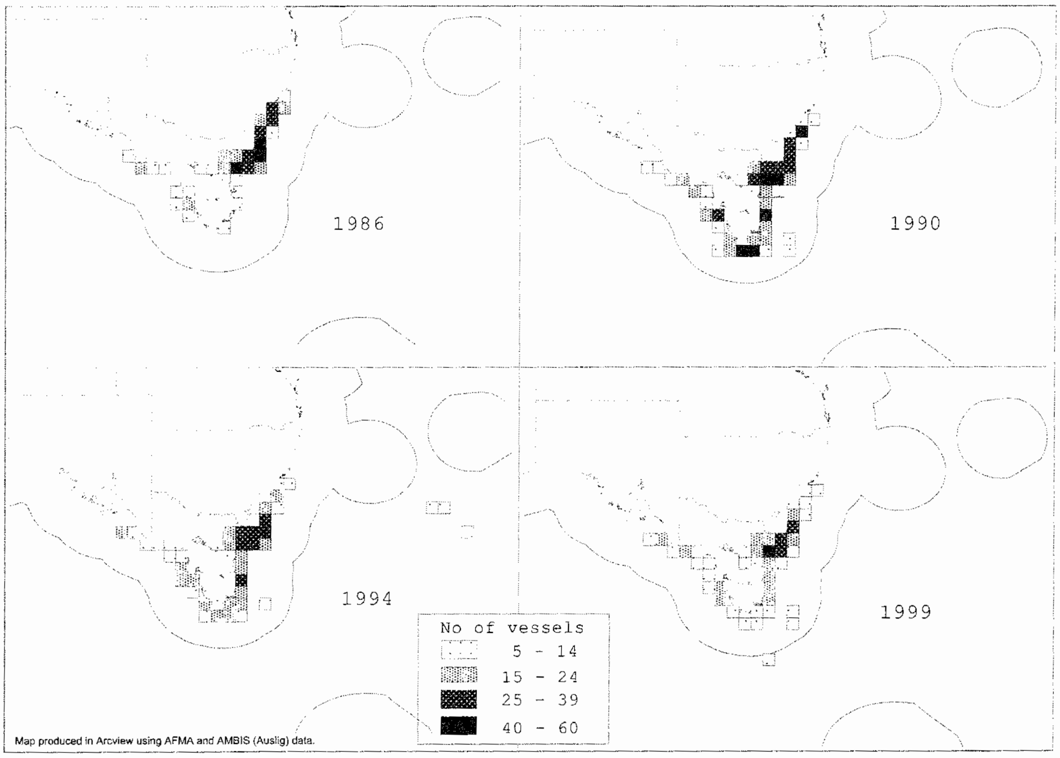


Fig. 2. Numbers of vessels recording a catch in the South East Trawl Fishery of Australia by 1° squares in 1986, 1990, 1994 and 1999. Source: AFZIS database (AFMA) and AMBIS data (Auslig).

---

[1] Input controls are restrictions placed on the amount of effort input to a fishery, for example by restricting the size of fishing gear and boats and the amount of fishing time. Output controls are restrictions placed on the quantity of fish that can be taken from a fishery within a specified period of time. This can be by either a competitive annual total allowable catch (TAC) or a TAC allocated to participants as ITQs.

Commonwealth (Federal) Fishing Boat Licences (CFBLs) was suspended, but by this time thousands of such licences were permitting access to scalefish by gill-net, demersal-line and trap methods in Federal waters. Many of these licences were not used to any great extent, creating a large pool of latent effort. In 1988, gill-net operators were brought under input controls that restricted fishing effort by a system of gear units designed to limit the take of school and gummy shark (Walker et al. 1998). This also had the effect of reducing the gill-net effort that could be directed at scalefish.

New directions

Trawl sector

During the mid to late 1980s the Federal Government was developing a policy for management of its fisheries and in 1989 released a policy statement ('New Directions') for the 1990s (Anon. 1989*b*). Fisheries economic theory and the emerging concept of ecologically sustainable development (ESD) were the main philosophical underpinnings of this document. Invoking economic theory about the benefits of property rights and output controls for reducing (or preventing) over-capitalization and over-exploitation, New Directions suggested that ITQs would lead to more rational economic and sustainable outcomes for fishing operators and society alike. Autonomous adjustment would be possible through the introduction of such a management regime – the more efficient operators would buy out the less efficient ones, the race for fish would not be necessary, fisheries would stabilize and resource rent would not be dissipated (Anon. 1989*b*).

The first fishery management regime to change under this new policy was the South East Trawl Fishery (SETF). On 1 January 1992 ITQs were introduced by the former Australian Fisheries Service, a division of the Department of Primary Industries and Energy, for 16 trawl species or species groups. In February 1992 the Australian Fisheries Management Authority (AFMA) was created under the *Fisheries Administration Act 1991* and inherited the new and highly controversial management plan for the fishery, the *South East Fishery (Individual Transferable Quota) Management Plan, 1991* which had been determined by the Minister under section 7B of the recently repealed *Fisheries Act 1952 (Cwlth).*

The ITQ management regime encountered problems at the outset. There was widespread dissatisfaction with the results of quota allocations, and in March 1992 the newly formed AFMA Board put a moratorium on permanent transferability of quota allocations while an independent review was conducted (Anon. 1996). In the meantime court action had been initiated by a fishing company against the allocation formula in a case called *Austral Fisheries Pty Ltd v Minister for Primary Industries and Energy* and a majority of quota holders had appealed to AFMA for internal reviews of their quota allocations. In the *Austral* case, the judge found that the allocation formula contained a statistical fallacy that produced an irrational result, that the formula was void in law and that the relevant provisions of the plan were capricious and irrational (Kaufmann *et al.* 1999). This decision was upheld on appeal to the full bench of the Federal Court (Kaufmann *et al.* 1999). The offending allocation formula was a combination of catch history and units of fishing capacity, but it was the method of incorporating the catch history component into the formula that the judge found to be at fault. In the original 'market share' formula, each operator's best five years of a six-year qualifying period were used. However, the total allowable catch (TAC) was split into five equal parts, and each part was allocated separately based on the percentage of an operator's first best year out of the total of every operator's first best year, and the same for the second year, and so on. The 'irrational' result of this is that if only one operator took a quota species in the first qualifying year, then that individual received one fifth, or 20%, of the quota allocated for that species.

The allocation formula was changed by AFMA to the 'averaging method', considered to be more rational and statistically valid, in October 1992. The averaging still used the same combination of catch history and units of fishing capacity, but the catch history component was based on the sum of each operator's best five years of catch history for a species as a percentage of the total of all operators' best five years of that species. Full (i.e. seasonal as well as permanent) transferability of quota was reintroduced in 1994.

Some input controls were retained after the introduction of ITQs, including a limit on the number of vessels and minimum mesh sizes. As only 16 species or species groups out of hundreds of organisms that come in contact with the trawl gear were managed through output controls, the remaining input controls were retained to provide some mechanism to manage 'non-quota' species. Until 1997, the maximum vessel length of 32 m (with the exception of the four vessels up to 45.7 m) was also kept for all but fishing for orange roughy *Hoplostethus atlanticus* and blue grenadier *Macruronus novaezelandiae* off Tasmania. This regulation was successfully challenged in the Federal Court in *Bannister Quest Pty Ltd v Australian Fisheries Management Authority* on the basis that restricting vessel length was contrary to AFMA's objective of pursuing maximum economic efficiency. AFMA removed the vessel length restriction from the management regime of the fishery.

Autonomous adjustment did not occur upon introduction of ITQs as predicted by some theorists. This may be related to two things: the initial freeze on permanent transferability of quota; and the resistance of operators who continued to appeal against their quota allocations. The Federal Government intervened in 1997 and provided up to $A6.9 million in adjustment funding. In accordance with recommendations made by the SEF Adjustment Working Group (Anon. 1996), 27 fishing permits had by February 1998 been bought out of the fishery. In addition, 17 operators received 'targeted financial assistance' in the form of a payment for the loss of asset value of fishing entitlements in the change to the ITQ system from the former input control regime (Anon. 1996). Two of the objectives of the adjustment funding were to free up quota units for purchase or lease by the remaining fleet to assist ongoing adjustment, and to remove effort from the fishery (Anon. 1996). A study commissioned by Agriculture, Forestry and Fisheries Australia (AFFA) is being undertaken to assess how well the adjustment programme met its objectives. A by-product of the programme was that almost six years after the introduction of the ITQ system there was an end to litigation against quota allocations.

Non-trawl sector

In 1992, with the commencement of AFMA and the legislation underpinning it, ~550 Fishing Permits were granted to previous holders of CFBLs allowing for the take of demersal scalefish by non-trawl fishing methods. At the same time, a trip limit for eastern gemfish was introduced in response to concerns about the stock.

In 1994, AFMA commenced developing more specific access criteria and long-term management arrangements for the non-trawl fishery. Specific concerns had been raised regarding the non-trawl catch of three trawl quota species: blue eye trevalla (*Hyperoglyphe antarctica*), blue warehou (*Seriolella brama*) and ling (*Genypterus blacodes*). After a lengthy consultative process, the access criteria were applied in October 1996, further limiting to ~160 the number of operators with access to the fishery.

Following further extensive consultations, TACs were set for the non-trawl sector and individual quotas were allocated on 1 January 1998 to non-trawl operators for the three key species, blue eye trevalla, blue warehou and ling. In contrast to the trawl sector of the SEF, the transition to ITQ management and the allocation of quota in the non-trawl sector was relatively free of litigation. In large part this was due to establishment by AFMA of an Allocation Advisory Panel (AAP) to provide recommendations on the split of the TACs for the three key species between trawl and non-trawl gear sectors, and on the most appropriate formula to allocate quota to individual non-trawl participants. The AAP was independent of AFMA and comprised a retired Federal Court judge, an economist working in South Australia, and a fisher based in New Zealand. The AAP was required to consult with interested persons before formulating its advice to AFMA. The AAP's recommendations were ultimately accepted by the AFMA Board.

There are now plans to expand the non-trawl ITQ system to cover the remaining 13 trawl quota species and to integrate the two sectors under a single statutory management plan.

Management objectives since 1992 – have they been met?

The objectives that must be pursued by the Minister in the administration of the *Fisheries Management Act 1991 (Cwlth)* ('the Act') and by AFMA in the performance of its functions can be found in section 3 of the Act (as amended, 1997):

(a) implementing efficient and cost effective fisheries management on behalf of the Commonwealth [of Australia];

(b) ensuring that the exploitation of fisheries resources and the carrying on of any related activities are conducted in a manner consistent with the principles of ecologically sustainable development and the exercise of the precautionary principle, in particular, the need to have regard to the impact of fishing activities on non-target species and the long term sustainability of the marine environment;

(c) maximising economic efficiency in the exploitation of fisheries resources;

(d) ensuring accountability to the fishing industry and the Australian community in AFMA's management of fisheries resources; and

(e) achieving government targets in relation to the recovery of the costs of AFMA.

Table 2. Total (industry and government) management costs of the South East Trawl Fishery, Australia, as a percentage of gross value of production (GVP)

Source: AFMA and ABARE (http://www.abareconomics.com/pubcat/fisheries.htm)

Year	GVP ($Amillion)	Management costs Total ($Amillion)	Industry ($Amillion)	Government ($Amillion)	Total costs (% GVP)	Industry costs (% GVP)
1995–96	53.177	2.807	1.955	0.852	5.28%	3.68%
1996–97	53.245	1.966	1.401	0.564	3.69%	2.63%
1997–98	57.701	2.805	1.708	1.097	4.86%	2.96%
1998–99	59.885	2.518	1.525	0.993	4.25%	2.58%

Efficient and cost-effective fisheries management

Management costs as a percentage of gross value of production (GVP) for the trawl sector have been relatively stable since 1995–96 (Table 2). An apparent reduction in 1996–97 was due to changes in the method of accounting for certain compliance costs and a subsequent roll over of costs into the following financial year; hence, this did not represent the real cost of managing the fishery in 1996–97 (P. Venslovas, personal communication).

AFMA has stated that management costs as a percentage of GVP is the measure of its performance in relation to its principal output (i.e. provision of fisheries management services). The question is whether this is an appropriate measure of AFMA's performance against its efficient and cost-effective fisheries-management objective. In considering the question of how cost effectiveness should be measured, we suggest that measuring actual outputs rather than solely costs against GVP may be more valid. Having said that, we also propose the following thoughts about outputs, which could confound one's thinking about efficient and cost effective management:

- over the past 10 years, government and other organizations have become smaller and yet the complexity of the job has increased, creating a working environment of doing more with less;
- demands on fisheries managers in Australia have increased, e.g. they include input on an ever-increasing range of conservation issues (e.g. environmental impact assessment, management of endangered and protected species, sustainability of export species and development of marine protected areas), reporting on transparent or accountable government and increased legislative responsibilities such as preparation of regulatory impact statements;
- the expectations of stakeholders in the electronic age have increased dramatically; with email and Internet access, fax and mobile telephone communication systems, information is now a premium commodity in the developed world.

In a truly competitive world perhaps the only real test of efficient and cost-effective management would be to open up the provision of fisheries management services to tender.

Ecologically sustainable development and the precautionary principle

The principal management strategies for pursuing ESD are the following: setting TACs for the 16 major species or species groups exploited in the fishery, allocating ITQs to operators, limiting entry to the fishery and maintaining minimum codend mesh sizes for otter-trawl and Danish-seine methods.

We have chosen not to address performance against this objective in any detail. Each year the South East Fishery Assessment Group publishes a report that assesses the fishery, trawl and non-trawl sectors, and the quota species primarily against the ESD objective (e.g. Tilzey 1998). *Marine and Freshwater Research* volume 52 issue 4 (2001) contains many scientific papers that also deal with the biology and assessment of quota species as well as papers about habitat and the ecosystem.

What has not been assessed in great detail in the past is the sustainability of by-catch species, both those retained (i.e. by-products of target fishing) and those discarded. A significant amount of data on retained and discarded by-catch species has been collected through a variety of research projects and scientific monitoring programmes (Knuckey *et al.* 1999). These data may contribute to assessing the sustainability of by-catch species; however, research is required into the development of cost-effective and practical sustainability indicators for these species, e.g. by monitoring and assessing particular species within the community structure as 'indicator' species.

Further research is required into the effects of fishing on the marine environment (specifically the effects of trawling on the habitat and ecosystem in the SEF), as well as the development of feasible indicators of ecosystem sustainability. Work by research agencies to fill these gaps has commenced in the SEF.

Stakeholders in the management process, i.e. industry, scientists, environmentalists and managers, have collaborated on the development of 'Bycatch Action Plans' for the SEF. The plans are intended to provide a holistic approach to by-catch management, with strategies including review of data collection programmes, setting of research priorities, development of alternative management arrangements and gear technology, market and post-harvest development and a communication/education programme.

Maximizing economic efficiency

In 1993 the Food and Agriculture Organisation of the United Nations estimated that it cost $US124 billion to harvest global fisheries resources valued at only $US70 billion (FAO 1993). A characteristic of many fisheries around the world is economic inefficiency, i.e. that scarce resources such as labour, capital, fuel and natural resources are wasted through over investment or over capitalization. In the context of a fisheries management objective, maximization of economic efficiency could be said to refer to the implementation of management arrangements that provide conditions that allow an entire fishery to move towards the greatest possible economic benefits from the limited resources available.

In reviewing management performance against the economic efficiency objective, as managers we are interested in the distinction, as well as the relationship, between allocative efficiency and productive efficiency. In allocative efficiency, scarce resources (natural resources, labour, capital and other inputs) are not wasted, or the goods that best meet society's needs are being produced. In productive efficiency (a subset of allocative efficiency), a given level of output is achieved with the least cost combination of inputs.

The challenge arises when trying to measure economic efficiency. How do management arrangements in a fishery affect the allocative and productive efficiency of the fleet? At a small workshop conducted in 1998 by the South East Fishery Assessment Group, economists and fisheries managers were unable to reach consensus on how, or indeed whether, economic efficiency should be measured. Participants were divided over the extent to which economic efficiency indicators were useful in a fishery managed through tradeable output controls (i.e. ITQs). Some argued that the introduction of ITQs allowed the pursuit of allocative efficiency, i.e. quota trading would allow those who most valued the quota to acquire it[2]. Others argued that the pursuit of allocative efficiency was only possible indirectly by encouraging productive efficiency through the management arrangements in place, i.e. where the least costs are incurred at an industry level in harvesting a given quantity of fish – for example by implementing ITQs and removing unnecessary input controls. It was the conclusion of the workshop that, in pursuing the objective to maximize economic efficiency, allocative efficiency can be pursued to the extent that productive efficiency is pursued. Even by reaching this position, workshop participants did not reach consensus on how to measure performance against AFMA's objective.

A few simple indicators of change

In the absence of modelling techniques or methods of measuring management performance against the economic efficiency objective, we looked at some basic fisheries information from the SETF in an attempt to see whether the management arrangements had minimized constraints, allowed flexibility or provided for adjustment in the fishery.

Tonnage of fish caught v. gross value of production. Two simple indicators of change are fish prices and the tonnage of fish landed. We assumed that, all things being equal, if the price of fish were going up while the weight of fish being landed remained constant or decreased, this would be positive for the fishery as a whole.

In the SETF, interpretation of the tonnage of fish landed and price received is made more complex by the relatively large and changing tonnage of one species, orange roughy (Fig. 3). The tonnage of orange roughy has decreased substantially over that period, from 37 901 t in 1989/90 to 4728 t in 1998/99, with a low of 3129 t in 1996/97. While the tonnage has decreased by 87% over this period, the value of orange roughy landings has fallen by only 69% from $A49.3 million in 1989/90 to $A15.2 million in 1998/99; the landed price for orange roughy has more than doubled over the ten-year period, with the most significant gains having occurred over the transition period, 1991/92 and 1992/93, from input controls to ITQ management (Fig. 4). The picture is a little less marked, but still positive, for all other species combined; a slight upward trend in the average price of fish (excluding orange roughy) from $A1.34 per kg in 1989/90 to $A1.91 in

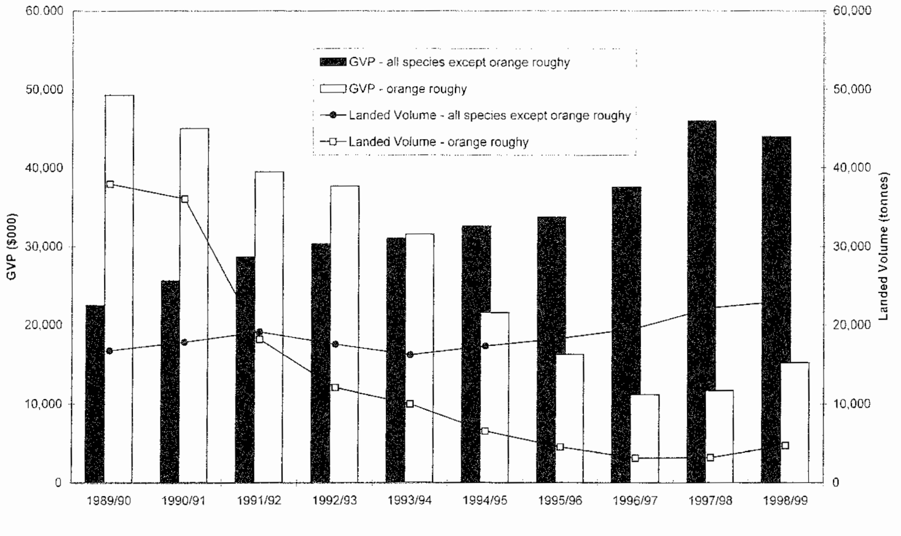


Fig. 3. Gross value of production (GVP) and landed volume for orange roughy and all other species combined in the South East Trawl Fishery from 1989/90 to 1998/99. Source: ABARE (http://www.abareconomics.com/pubcat/fisheries.htm)

---

[2] For an investigation into the trading of quota in the fishery, see Connor and Alden (2001).

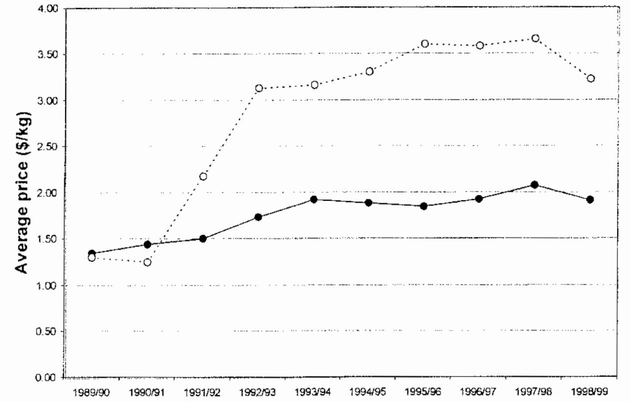


Fig. 4. Average price of fish for (○) orange roughy and (●) all other species combined in the South East Trawl Fishery from 1989/90 to 1998/99. Source: ABARE (http://www.abareconomics.com/pubcat/fisheries.htm)

1998/99 with a high of $A2.07 in 1997/98 (Fig. 4) has been gained against a background of an increase in landed tonnage from 16 729 t in 1989/90 to 23 022 t in 1998/99 (Fig. 3). This results in significant gains in the gross value of production for these species from $A22.5 million in 1989/90 to $A44.0 million in 1998/99.

These simple indicators of change could send a positive message about the fishery's performance. Clearly this is only a good result if the cost of catching the higher tonnages of fish is not so high as to negate the higher returns. Further investigation may be required to clarify whether the signals from these data do reflect positive performance in the fishery, e.g. establishing the extent to which prices reflect cost-of-living increases, changes in species composition (hence relative price), or changes in demand *v.* availability.

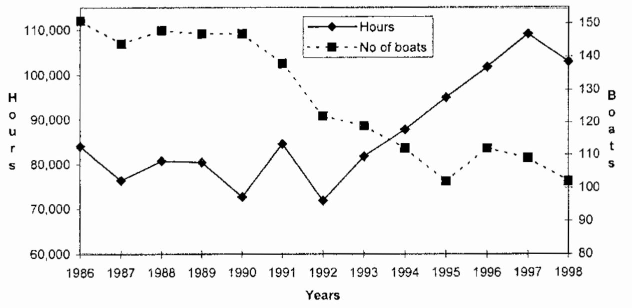


Fig. 5. Effort in the South East Trawl Fishery 1986–98: boat numbers and hours trawled. Source: AFZIS database, AFMA.

Vessel numbers and hours trawled. Between 1986 and 1991, under the input control regime, the number of vessels actively fishing in the trawl fishery (i.e. boats that recorded a catch on logbooks in the calendar year) declined from 151 to 138 (Fig. 5). Between 1992 and 1998 vessel numbers continued to decline from 122 to 102. One might expect to see a corresponding decreasing trend in hours trawled as recorded on logbooks inside the Australian Fishing Zone, but this is not the case (Fig. 5). The trend in hours trawled between 1986 and 1992 is relatively stable, fluctuating between ~70 000 and ~84 000 h, and the trend after 1992 shows a significant increase to a peak in 1997 of ~108 000 h followed by a slight reduction in 1998.

On the face of it this means that the cost of inputs to fishing (e.g. fuel and other material inputs) should be higher, contributing to lower financial performance overall. Prince *et al.* (1998) describe the changes in fishing patterns of operators since the introduction of ITQs. Operators are no longer fishing for large tonnages of one or two species in a

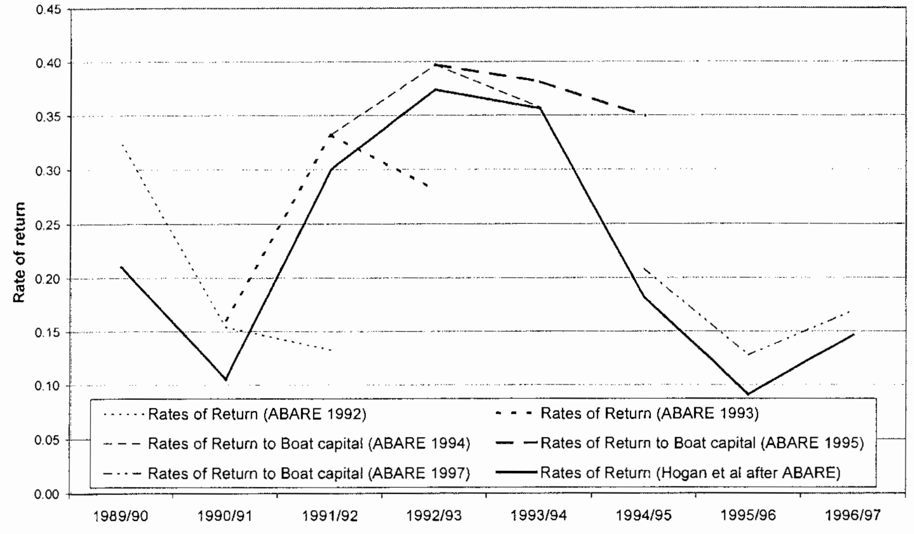


Fig. 6. Rates of return to capital for the South East Trawl Fishery, 1989–90 to 1996–97. Sources: Brown (1997), previous Australian Fisheries Surveys Report issues (http://www.abareconomics.com/pubcat/fisheries.htm) and Hogan *et al.* (1999)

short space of time, but rather for a greater range of species. Whether this change was brought about by markets beginning to demand greater variety of higher-quality product, or by operators beginning to fish to fill their quotas, or by a combination of both, or by other factors is still the subject of debate.

In the context of our examination of some simple indicators of change to gauge performance of the fishery as a whole, the question remains, are the gains made in landed value of product more than offset by the higher cost of catching the fish?

Rates of return. The Australian Bureau of Agricultural and Resource Economics conducts economic surveys of the fishing industry and has developed a database of information that provides indicators of financial or economic performance of fisheries. The SETF has been the subject of such surveys (http://www.abareconomics.com/pubcat/fisheries.htm; Brown 1997). The absolute values in the survey calculations have changed with each publication, hindering interpretation by fisheries managers with limited economic expertise. Using the rates of return to capital from these publications and from Hogan *et al.* (1999), where rate of return is calculated by expressing profit at full equity as a percentage of total capital (excluding quota and licence values), Fig. 6 shows a decline to 1990–91 and an increasing trend to 1992–93, followed by a decline. The declining trend after 1992–93 appears to indicate that the higher cost of catching fish more than offsets the higher returns in the fishery in recent years.

Conclusion

In attempting to measure the performance of the SEF against fisheries management objectives we have focussed most of our attention on the major milestone in the trawl sector of the fishery in the past decade, the move from input controls to the ITQ management regime. We have not addressed the question of performance against AFMA's legislative objective to ensure that the fishery is exploited in a manner consistent with the principles of ecologically sustainable development. In our quest to understand whether management had met objectives we have placed most of our attention on the economic efficiency objective. Having been through the exercise of putting together some simple indicators of change in the fishery, we are left with more questions than answers.

Economic performance in the SEF appears to have peaked in the early 1990s and declined more recently to a level consistent with that before the introduction of ITQs. The question for us as managers is, would the fishery be relatively better off or worse off if ITQ management had not been introduced? In the absence of this major management intervention, would rates of return be plummeting? These questions can never be answered.

In relation to performance against the economic efficiency objective, should allocative efficiency or productive efficiency be measured? Should we be measuring the removal of impediments to operators' choice of how, why and where they go fishing? Measured against the removal of impediments that are not related to the pursuit of the ESD objective, the management of the fishery could be said to be consistent with the economic efficiency objective. Alternatively, should we be measuring the collective reaction of individuals in the fishery as determined by financial performance surveys? With the data available, in absolute terms, the picture does not appear as positive.

Finally, in our musings about whether the SEF was living up to the expectations set out in *New Directions*, another of our questions came to the fore: After nearly 90 years of supplying fresh fish to the Australian consumer and only eight years with ITQ management, is it still too early to tell?

Acknowledgments

For ideas and some words we acknowledge the following people: Dave Alden (Australian Fisheries Management Authority), Sean Sloan (South Australian Department of Primary Industries), Dave Johnson (National Oceans Office), Dave Smith (Marine and Freshwater Resources Institute, Victoria) and Gerry Geen (Fisheries Economics, Research and Management Ltd).

References

Anon. (1989*a*). Management of the South East Trawl Fishery: a report of an Australian Fisheries Council Sub-Committee. (Department of Primary Industries and Energy: Canberra.)

Anon. (1989*b*). New Directions for Commonwealth Fisheries Management in the 1990s. A government policy statement. (Department of Primary Industries and Energy: Canberra.)

Anon. (1996). Report of the South East Fishery Adjustment Working Group. To the Minister for Resources and Energy. (South East Fishery Adjustment Working Group, Department of Primary Industries and Energy: Canberra.)

Brown, D. (1997). Australian fisheries surveys report 1997. (Australian Bureau of Agricultural and Resource Economics: Canberra.)

Connor, R., and Alden, D. (2001). Indicators of the effectiveness of quota markets: the South East Trawl Fishery of Australia. *Marine and Freshwater Research* **52**, 387–97.

FAO (1993). Marine fisheries and the law of the sea: a decade of change. (Food and Agriculture Organisation of the United Nations: Rome.)

Geen, G., Brown, D., and Pascoe, S. (1991). Restructuring the South East Trawl Fishery. In 'Proceedings of the Australian and New Zealand Southern Trawl Fisheries Conference: Issues and Opportunities. Melbourne'. (Eds K. Abel, M. Williams and P. Smith.) pp. 129–41. (Bureau of Rural Resources: Canberra.)

Hogan, L., Thorpe, S., and Timke, D. (1999). Tradable quotas in fisheries management: implications for Australia's south east fishery. Report to the Fisheries Resources Research Fund. (Australian Bureau of Agricultural and Resource Economics: Canberra.)

Kaufmann, B., Geen, G., and Sen, S. (1999). Fish Futures: individual transferable quotas in fisheries. (Fisheries Research and Development Corporation: Canberra.)

Klaer, N. L. (2001). Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. *Marine and Freshwater Research* 52, 399–410.

Knuckey, I. A. Grieve, C., and Smith, D. C. (1999). Evolution of the integrated scientific monitoring programme in Australia's South East Fishery. In 'Proceedings of the International Conference on Integrated Fisheries Monitoring, Sydney'. (Ed. C. P. Nolan.) pp. 231–48. (FAO: Rome.)

Lack, M. (1991). Changing policy requirements of the South East Trawl Fishery. In 'Proceedings of the Australian and New Zealand Southern Trawl Fisheries Conference: Issues and Opportunities, Melbourne' (Eds K. Abel, M. Williams and P. Smith.) pp. 190–94. (Bureau of Rural Resources: Canberra.)

Lyle, J. M. (1994). Orange roughy, *Hoplostethus atlanticus*. In 'The South East Fishery: a Scientific Review with Particular Reference to Quota Management'. (Ed. R. D. J. Tilzey.) pp. 98–114. (Bureau of Resource Sciences: Canberra.)

Menz, K., Geen, G., and Collins, D. (1986). Issues in the management of the South-east Trawl Fishery. Discussion Paper 86.2. (Bureau of Agricultural Economics: Canberra.)

Prince, J., Baelde, P., and Wright, G. (1998). Synthesis of industry information on fishing patterns, technological change and the influence of oceanographic effects on SEF fish stocks. (Fisheries Research and Development Corporation: Canberra.)

Rowling, K. R. (1994*a*). Gemfish, *Rexea solandri*. In 'The South East Fishery: a Scientific Review with Particular Reference to Quota Management'. (Ed. R. D. J. Tilzey.) pp. 115–23. (Bureau of Resource Sciences: Canberra.)

Rowling, K. R. (1994*b*). Tiger flathead, *Neoplatycephalus richardsoni*. In 'The South East Fishery: a Scientific Review with Particular Reference to Quota Management'. (Ed. R. D. J. Tilzey.) pp. 124–36. (Bureau of Resource Sciences: Canberra.)

Smith, D. (1991). South eastern trawl fishery: inshore resources. In 'Proceedings of the Australian and New Zealand Southern Trawl Fisheries Conference: Issues and Opportunities, Melbourne'. (Eds K. Abel, M. Williams and P. Smith.) pp. 241–50. (Bureau of Rural Resources: Canberra.)

Tilzey, R. D. J. (1994). The South East Fishery: a scientific review with particular reference to quota management. (Bureau of Resource Sciences: Canberra.)

Tilzey, R. (1998). South East Fishery Assessment Group Fishery Assessment Report. (Australian Fisheries Management Authority: Canberra.)

Walker, T. I., Johnstone, D., Brown, P., and McLoughlin, K. (1998). The Southern Shark Fishery 1997. Fishery Assessment Report, Southern Shark Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Manuscript received 15 May 2000; revised and accepted 23 January 2001

Mar. Freshwater Res., 2001, **52**, 387–97

Indicators of the effectiveness of quota markets: the South East Trawl Fishery of Australia

Robin Connor[A] *and Dave Alden*[B]

[A]Centre for Resource & Environmental Studies, Australian National University, Canberra, ACT 0200, Australia
[B]Australian Fisheries Management Authority, Box 7051, Canberra Mail Centre, ACT 2610, Australia

Abstract. This paper presents some results of an investigation into potential indicators for the assessment of markets for individual transferable fishing quota where price data do not exist. The economic logic for implementing such markets and how they are expected to work is used as a basis for asking questions about how well they are performing, and what might comprise evidence of problems. Given data on quota ownership, transfer and leasing, and associated catches, but no quota price data, indicators are suggested for monitoring and analysing market activity. These are applied to data from the Australian South East Trawl Fishery. Results are discussed in terms of the utility of the methods and the implications for management policy for the fishery.

Introduction

Many implementations (and even discussions) of tradeable rights schemes in fisheries access are contentious, even more so than other management initiatives. Much criticism and complaint with regard to individual transferable quota (ITQ) systems remain unsubstantiated by systematic investigation, as do many of the claimed benefits. The decentralized decision-making system that a quota market provides contributes further complexity of detail and interaction to already complex fishery systems. Ecological, economic, technical and social factors interact to produce highly individualized outcomes for fishing operators. The dynamics of individual circumstances and observed trends in particular aspects of the fishery interact further with disparate mental models of how these complex systems really work, and inevitably give rise to an array of hypotheses and prescriptions for policy.

In order to make progress on understanding the issues more clearly, complexity needs to be reduced by investigating aspects of the system somewhat independently, while not loosing sight of the interdependencies. The dynamics of quota markets is one area for which methods of investigation have not been greatly developed. This paper reports on a simple indicator-based approach to assessment and monitoring of quota markets, based on quota ownership, quota trade, and catch data from the Australian South East Trawl Fishery (SETF). Rudimentary analysis of management agency data is used to investigate trends in the development of the quota market and fishery system. Some policy implications of these trends are discussed.

Before presenting the analysis, we provide a discussion of the general rationale for creating a market in rights, and discuss how such a market is expected to function. We focus on the expected dynamics of a quota market, and do not attempt to discuss the particular choice to establish ITQs in the SETF. The study takes the quota system as a given, and attempts to establish whether the quota market is performing as might be expected, or if there seem to be impediments to its operation. The general characteristics of the SETF and its quota management system are reported elsewhere in this issue (Grieve and Richardson 2001; Smith *et al.* 2001; Tilzey and Rowling 2001) and will not be elaborated in detail here.

Rights markets in fisheries management

Transferable rights systems have been widely used for the allocation of scarce resources. The key objective in using this management instrument is to improve economic efficiency by allowing resources to flow to their highest valued use through market transactions. Examples of working systems range from transferable taxi licences (Tullock 1975), agricultural production quotas such as the transferable milk quota system in the UK, to air and water based emissions trading (Tietenberg 1995; Smith 1999), ground and surface water allocation (Colby 1995; Bjornland and McKay 1998), and fisheries quotas (for review and bibliographies see (OECD 1993; ICES 1996; NRC 1999).

The basic static bioeconomic model underpinning much fisheries management policy is well known (Gordon 1954; Scott 1955; Arnason 1993; Conrad 1995; Hartwick and Olewiler 1998). This predicts that unrestricted access to fisheries resources will result in the dissipation of all

10.1071/MF99164 1323-1650/01/040387

potential economic rents[1], and that characteristics of costs and prices will determine an equilibrium at which both the biological and economic yield may be well below their potential maxima. Under technically efficient harvesting and high market demand for fish, stocks may be pushed passed ecological thresholds from which they do not recover when fishing pressure is removed, the so-called 'Allee effect' (May 1976).

The economic prescription for this malaise is the better definition of access rights to the fishery. Whereas other regulatory controls attempt to constrain economic inputs, tending to restrict technical efficiency (Menz *et al.* 1986), fish quota mechanisms such as ITQs allocate quantified shares in the potential catch and allow fishers to decide the least cost method of harvest. ITQs are implemented in combination with a Total Allowable Catch (TAC), which serves as an aggregate cap on extractions. Under a TAC without quotas, individual operators have an incentive to compete for as much of the available catch as they can land before the TAC is filled. This race for fish encourages excessive investment in vessels and equipment, and can lead to dangerous practices, short seasons, and market pulses with associated poor prices and lack of continuity of supply (Terry 1993). In addition, competitive TACs are difficult to control, and have a history of over-runs. Even when entry to such a fishery is restricted, the economic result tends to that of open access.

Whether transferable or not, individual quota under a TAC defuses the race for fish otherwise generated by the cap. With secure rights to a share of the catch, fishers are more able to plan for fishing over the whole season, and to adapt their approach to timing, technology, crew and numerous other factors, to maximize the economic surplus from the catch. This can mean a steadier supply of fish, possibly of higher quality realizing better prices, and it should minimize over-investment (Moloney and Pearse 1979; Copes 1986; Casey *et al.* 1995[2]). If individual quota is made transferable, this enables the right to take fish to move between potential harvesters, at prices that reflect expected gains for both parties[3]. Being a divisible right, just the amount of harvest right desired can be transferred or leased from one operator to another, allowing individuals to optimize their existing fishing operations, or to enter or exit the industry where they believe that is in their best interests. Long-term or in-season adjustment of quota holdings to match catches may be carried out by trading or leasing. Under conditions of short-term uncertainty, leasing may be preferred.

Fishers that profit most from holding ITQs (the most efficient) should be willing to pay the most in a market for quota, if additional units are required. All operators have an incentive to improve the rate of return on their quota through pursuing practices that reduce costs of fishing and increase the value of fish sold. A positive feedback effect can occur as quota market values increase in response to increases in fleet efficiency. This places further incentive on fishers to increase net income per tonne of ITQ so as to be able to afford to lease in quota when required, and to match increasing opportunity costs of the capital value of their quota. This may be achieved by adjusting existing operations to fully use vessel and gear capacity, adopting new technology, and through improved marketing, value-added processes, or different modes of business organization. Such pressures to increase income may also result in an increase in rule breaking such as fish discarding, including high-grading, and quota busting (see Copes 1986). Compliance is generally difficult and expensive to enforce at sea, and even assessment of the extent of such problems is difficult.

The least efficient operators may face a situation where the realizable capital value of their ITQ holdings will produce more income in an alternative investment, outside the fishery. Whether they choose to sell up and exit the fishery may depend on a range of factors, including the resale value of other capital assets such as vessels and gear, alternative employment prospects, and other values they hold for continued participation. However, choosing to stay in the fishery under these circumstances will mean that leasing in quota may become prohibitively expensive.

Often, quota systems are prescribed where a problem of over-capacity has already developed. The reduction of this capacity to achieve efficiency gains implies a need for some fishers and vessels to exit the fishery. A rights market allows the impact of this adjustment on individuals and communities to be mitigated through allowing self-selection of exiting units, and through the realization of capital from

---

[1] Economic rents are profits from an activity over and above all costs. Costs here include normal returns to capital and labour.

[2] Casey *et al.* report on British Columbia's fishery for halibut where individual vessel quotas (IVQs) were introduced in 1991. Immediately before the regulatory change, this fishery was a classic derby fishery. The season had been reduced to 60 days per year with each vessel allowed only six days of fishing each season, such was the excess capacity of the fleet. Virtually all product was sold frozen with the annual supply glut depressing prices and hurried fishing and handling resulting in much damaged fish. Following introduction of IVQs, landings have been spread out over an eight-month season with 94% of product now sold as fresh, resulting in an average price premium of over 50%.

[3] The willing-buyer-willing-seller assumption is subject to failure in various circumstances; for example, where market power is used to control distribution channels. Prices of both fish and quota can also be manipulated, reducing the viability of catching operations and thereby forcing sales under pressure of debt servicing and so on.

the sale of rights. Hence the market becomes a means for compensated and voluntary rationalization of capacity.

A framework for assessment

Failure of the quota market to function well may mean that much of the potential for efficiency gains remains unrealized, and it may also have consequences for conservation goals. In order to approach assessment of a quota market, an understanding of what might go wrong is required. Efficiency in markets hinges on a range of conditions being met. These include the following:

- well defined and protected rights;
- many buyers and sellers;
- good quality and freely available information; and
- low transaction costs.

Where information is incomplete, rights cannot be precisely defined and secured. ITQs that allocate a proportion of the TAC each year to quota shares, as in the SETF system, are constituted that way specifically because of the uncertainty surrounding the state of stocks and their future. Although the fact that the right is a share of whatever is available each year can be clearly stated, the effectiveness of the right itself is diluted in economic terms due to its uncertain future value. The degree to which rules that support rights are enforced can also affect market outcomes by altering expectations and prices. Competitive markets by their nature tend towards elimination of the requirement of many participants. The accumulation of a degree of ownership dominance by one entity, or a group that can co-operate, such that their actions can affect prices, will compromise efficiency gains.

Information is the life-blood of markets. In fact it is the ability of markets to incorporate huge amounts of diverse information into allocation outcomes that makes them valuable. Lack of channels for key types of information, or asymmetries in information access between market participants, will lead to distortions. The costs of search time and effort for information relating to market decisions can be included in the category of transaction costs, and if significant will have an inhibiting effect on trade. Markets that involve large disparities in the size of firms—for example, ranging from owner-operator vessels to large companies contracting catching capacity—are likely to involve scale economies in overcoming both information problems and other transaction costs. A large firm with full time administrative and professional staff will generally find it cheaper on a per tonne basis to locate and negotiate the lease or purchase of required quota than a small firm.

The empirical section of this study uses the above basic assumptions of market theory in developing an analysis of the effectiveness of a quota market using ownership, trading and catch data from the SETF. We do not address the definition of fishing rights in the SETF directly, as this has many dimensions for which direct impacts on trading and ownership patterns would be difficult to detect from available data. The focus here is on aspects of the data that might speak to the issues of information asymmetry and transaction costs in particular, and briefly to the issue of competitiveness. First we look at aspects of market participation as evidence that quota owners have sufficient information and knowledge to use trade when it is in their interests to do so. We also look for evidence here for the effect of transaction costs on participation. The issues of quota 'landlording' and quota concentration are examined for scale that might lead to the development of market power. We then present an original analysis that looks at the match of catch against quota holdings, and how this changes over time, again looking for evidence of possible asymmetries in transaction costs and information.

The South-East Trawl Fishery quota market

Individual transferable quota was introduced to the SETF in January 1992 covering 16 species (or species groups) in 19 stocks (orange roughy has three quota stocks and gemfish has two). The fishery is a mixed trawl fishery with three method sectors: danish seiners, inshore otter trawl and deepwater trawl. The fishery has had ~100–120 operating vessels in the period since 1992, with 50–60% of the fleet in the inshore otter trawl sector. The nature of mixed trawl fisheries is such that the ratio of species caught in any one trawl, trip or season is not entirely predictable, and highly variable environmental conditions off the south-eastern corner of Australia make the SETF particularly unpredictable at the individual operator level (Prince *et al.* 1999). This poses particular problems for the operation of the fishery under quota constraints (Squires *et al.* 1998). The Australian Fisheries Management Authority (AFMA) is the agency responsible for managing the fishery, and maintains registers of quota ownership. All quota sale and lease transactions are subject to approval of AFMA, but reporting prices is not a requirement. The following analysis uses data supplied from the AFMA quota management system.

Quota market participation

Basic to the achievement of market-mediated objectives for the fishery is the need for quota holders and fishing operators to have access to, and to participate in, trade. As price data are not available for the SETF quota system, numbers and volumes of lease and permanent transfer transactions provide a starting point for examining trading activity. Detailed statistics on SETF quota trading volumes by year and species have been provided by Hogan *et al.* (1999). Count and volume statistics for leases and permanent trades are summarized in Table 1, and participation is summarized in Table 2.

The number of lease transactions in the fishery has more than doubled in the period 1992–98. Total lease volumes declined with the decline in orange roughy landings to 1996.

Table 1. Transaction summary of SETF quota market 1992–98
Data source: AFMA

Quota transactions	1992	1993	1994	1995	1996	1997	1998
No. of leases (no co-op)	878	969	935	1092	1288	1444	1831
Lease volume (no co-op) (t)	17245	15286	12832	11311	12386	14990	24668
Lease volume as % of catch	61%	66%	67%	62%	67%	73%	120%
Agreed^A TAC (t)	34765	31665	33465	34165	33165	31965	32360
Allocated^A TAC (t)	36220	33902	40429	40673	40350	38186	37492
Total catch (t)	28485	23325	19275	18352	18588	20395	20599
No. of permanent transfers	133	146	446	134	112	67	230
Permanent transfer volume (t)	1365	3102	6084	1916	868	628	5258
Cumulative transfers as % of agreed TAC	4%	14%	32%	37%	40%	44%	59%
No. of blue grenadier permanent transfers	12	9	25	6	5	3	41
Volume of blue grenadier permanent transfers (t)	181	465	1459	266	173	50	3798

^{A}Owing to the operation of quota carry-over provisions, the TACs set by the management agency on agreement with stakeholders (Agreed TAC) is not usually the same as the total of all entitlements to catch fish for the year (Allocated TAC). The Allocated TAC takes into account up to 20% of individual holdings that can be carried over from the previous year if they have been either over- or under-caught. If the total carryover of under-caught quota exceeds carry-over of over-catch for a species, the Allocated TAC will exceed the Agreed TAC.

Underlying this are increasing lease volumes for ling and redfish in particular, following steady increases in the TACs; see Hogan *et al.* (1999) for more detail. In 1997 and 1998, blue grenadier volumes markedly increased as a result of some major permanent transfers of quota[4]. Non-co-operative[5] lease volumes have been consistently around two-thirds of the total catch until 1998.

Participation in quota leasing has steadily increased since the introduction of ITQs (Table 2). In 1998, 96% of all quota clients participated in the lease market, up from 54% in the first year of the system. A majority of lease market participants have been leasing quota both in and out over the period, suggesting that leasing is used extensively for balancing holdings across the variable mix of species. The total number of clients (owners and/or holders of quota) has increased some 36% over the 1992–98 period (Table 3), from about the same as the number of operating vessels, to 50% greater than the number of vessels in 1998. This diversification of ownership strategies suggests that the system has been keenly adopted by stakeholders.

As an initial indication of the use to which the SETF quota market is being put, the figures for trading activity show an active and growing market for annual quota leases. It seems clear that the lease market is proving useful to operators, given the overall catch constraints and the current distribution of permanent quota.

Permanent transfer v. lease

The question arises as to why there are not more permanent trades made, which might lessen the need for such large volumes of annual lease. As noted by Hogan *et al.* (1999), it has been common for packages of quota to be sold rather than individual species lots, although this does occur. The trend in permanent trades shows a surge in 1994, which was the first full year in which individual species quota could be sold (see Table 1)[6]. Smoothing the 1994 volume over the first three years, a reasonable assumption would be that the underlying need for adjustment was served in that period, with some ongoing but lower level of permanent trading

---

[4] Permanent quota sales transacted during a season do not take practical effect until the start of the following fishing year when new start balances are calculated. Often, as part of the transaction, uncaught portions of the quota are leased from the seller to the buyer to cover the current year. This means that when large changes in permanent holdings take place, matching lease volumes may appear in the year of sale.

[5] The Lakes Entrance Fishermen's Co-operative operates a quota redistribution scheme for their members who operate Danish seiners fishing for flathead and school whiting. Members' quota holdings are leased into the co-op. account at the start of the fishing year and leased back out on a monthly basis as required to match catch levels. These double leases are omitted here because the majority of this quota is leased back to the owners.

[6] Following the first quarter of 1992, during which permanent transfers of quota of individual quota were permitted, permanent sales of quota were restricted to whole packages for the first two years of the system, pending the outcome of legal challenges to the management plan, review of the initial allocation formula, and hearing of appeals against specific allocations by the Administrative Appeals Tribunal. Keeping packages together meant that any adjustments to the allocation mix could be more easily made if required. The allocation formula was reworked following review and quota holdings adjusted.

Table 2. Participation in SETF lease market 1992–98
Data source: AFMA

Market participation	1992	1993	1994	1995	1996	1997	1998
No. of lessees	57	65	80	102	106	101	118
No. of lessors	60	88	97	111	118	124	141
Total no. of participants	64	92	105	129	133	135	156
Total no. of clients	119	118	140	147	155	156	162
Participation rate							
Overall	54%	78%	75%	88%	86%	87%	96%
Leasing in	48%	55%	57%	69%	68%	65%	73%
Leasing out	50%	75%	69%	76%	76%	79%	87%
Leasing in & out	45%	52%	51%	57%	59%	58%	64%

Table 3. SETF sleeper quota holdings
Data source: AFMA

Zero catch and lease	1992	1993	1994	1995	1996	1997	1998
Number of quota stocks	18	19	19	19	19	19	19
Total clients	119	118	140	147	155	156	162
Total actual client-stocks	1429	1511	1562	1615	1699	1705	1776
Sleeper client-stock holdings	265	235	337	309	316	309	239
Number of sleeper holdings as a proportion of total	19%	16%	22%	19%	19%	18%	13%
Sleeper holding volumes (t)	830	500	3543	3487	2935	2643	1502
Sleeper holding volumes as % of allocated TAC	2%	1.5%	9%	9%	7%	7%	4%

activity continuing[7]. As indicated, the cumulative (all years) total volume of quota permanently traded amounts to 59% of the agreed TAC in 1998.

There are several reasons why repeated annual leasing may be preferred over permanent trade, but in general this can be taken as an indicator of uncertainty. In a mixed trawl fishery such as the SETF, significant variability in catch mix is experienced from year to year by individuals. This uncertainty about quota requirements makes extensive use of leasing inevitable. A high degree of uncertainty also exists in stock estimates, and therefore in whether TACs accurately reflect management objectives (Tilzey and Chesson 1997). This is likely to make operators wary of permanent transfers, as the TACs could be subject to potentially large changes as new information comes to hand.

Another key issue for the adjustment of quota ownership in the SETF is that of sunk costs[8]. Where there are few other opportunities for the useful deployment of fishing vessels and gear, the resale value of these assets may be well below depreciated replacement cost. This effectively writes down the value of the boat to the level that, combined with the market value of owned quota, reflects the returns to the business at a rate offered by the next best investment. If there is no other use for the boat, it is not until this implicit valuation reaches the salvage value that it may become economically rational to exit the fishery and sell quota. However, owner-operators are also employed by their businesses, as may be members of their families, and in many areas alternative employment offering similar total benefits is hard to find. A choice to exit, although characterized by economists as being taken at the margin (of industry efficiency) and is therefore small, incremental and reversible, would be a large and irreversible decision for many individuals. In an uncertain environment these are more heroic than economic choices (Daly and Cobb 1994).

Weninger and Just (1997) investigated the relationship between uncertainty about the future value of quota and decisions to delay exit from an ITQ fishery. They found that lower salvage value for businesses (opportunity costs) and lower discount rates provide a greater incentive for inefficient operators to delay exit, because the pay-offs of waiting for a small increase in quota price can remain positive even where average total costs are very high. Hence, in the SETF, the combination of uncertainty over stocks, and therefore the appropriateness of TAC levels, and lack of alternative fisheries to move to may tend to lock-in existing vessels for the duration of their serviceable lives. Combined with the fixed number of permits in the SETF,

---

[7] High volumes of blue grenadier permanently transferred in 1998 largely account for the abrupt halt in this trend.

[8] This issue is also referred to as asset fixity, and as low opportunity costs of fixed capital.

this may effectively lock out new entrants wanting to deploy alternative fishing strategies. In fact, overall vessel numbers in the fishery have remained more or less static since the introduction of ITQs. A significant structural change over this period has been the shifting of vessels from the deepwater back into inshore trawling following the decline of the orange roughy fishery, but the total number of vessels has declined only slightly from 122 to fluctuate to between 102 and 112 in recent years (see Grieve and Richardson 2001 for more detail).

Although linked in some cases, the restructuring of quota ownership is generally not directly coupled to fleet rationalization. Efficiencies in the production and marketing chain other than in catching costs may dictate changing ownership patterns under quota without necessarily changing fleet configurations or even which boats and crew catch the fish.

Sleeper holdings

Sleeper holdings are those client–stock–year instances for which no catch and no lease activity are recorded (Table 3). In 1993 the average sleeper holding was ~2 t, and this increased to >11 t and then back to 6 t in 1998. These averages reflect the large unfished holdings of blue grenadier accumulated from the doubling of the TAC in 1994. However, underlying this is a large number of very small holdings that are unlikely to be thought worth the effort required to sell them. Some management action could be justified to overcome transaction costs for small holdings by offering stakeholders an opportunity to pool unwanted holdings that could then be auctioned.

Quota 'landlording' and concentration of ownership

Quota landlording is a concern often raised when ITQ management is being considered. Quota landlords do not fish, but own quota and lease it out for others to catch. Concerns arise from a range of perspectives, including the incentives for ecological stewardship, changes to labour relations, and, in combination with concentration of quota ownership, the development of market power (NRC 1999). Aggregates of ownership and leasing data can indicate the degree to which quota landlording is occurring, and whether this is changing over time. The following analysis is based solely on agency records, not taking into account the fact that individual interests in the fishery may have several quota accounts. In this study, each account is treated as a separate client, and we recognize that this means that some confounding factors are present.

In assessing the SETF data, we have distinguished two classes of landlord: Stock Landlords (SLs) are those quota owners that do not report catch for a stock for which they own quota, and whose holdings for that stock at year's end are at least 100 kg less than they own; and Pure Landlords (PLs) who are those quota owners that do not report catch for any species, and lease quota out. PLs are a subset of SLs. SLs who are not PLs are reporting catch for some stocks but hold and lease out other stocks for which no catch is taken. The aggregates given are of just the uncaught stocks.

Table 4 shows a fairly static picture of quota landlording with respect to most aggregates over the period before 1998. It is clear that most landlording is done by PLs, with the remaining SLs likely to be fishers who have changed target species (temporarily or otherwise) and have not sold their quota but lease it out instead. In 1997, for example, ~75% of the leasing of unfished holdings was carried out by PLs, representing ~25% of the total catch in the fishery. Other SLs leased out about another 6% of the catch. The one trend is the increasing number of PLs. The ease with which companies that are not harvesters can buy and own quota has been enhanced with the recent move to grant Statutory

Table 4. Quota 'landlording' in the SETF
Data Source: AFMA

Quota 'landlording'	1992	1993	1994	1995	1996	1997	1998
Total owned by SLs[A] (t)	7002	6377	6438	6187	6385	6568	10005
Total leased out by SLs (t)	6356	6202	5822	5109	5828	6324	8607
Total retained by SLs (t)	645	175	617	1078	557	244	1398
Total owned by PLs[B] (t)	4145	3637	4895	5028	5046	4826	8968
Total leased out by PLs (t)	3833	3600	4343	4116	4608	4683	7718
Total retained by PLs (t)	312	37	552	912	438	143	1250
PL retained as % of owned	8%	1%	11%	18%	9%	3%	14%
Number of PLs	12	11	29	31	28	35	42
% of TAC owned by PLs	11%	11%	12%	12%	13%	13%	24%
% of catch leased out by SLs	22%	27%	30%	28%	31%	31%	42%

[A] SLs: Stock Landlords are those quota owners who do not report catch for a stock for which they own quota, and whose holdings at year's end are at least 100 kg less than they own.

[B] PLs: Pure Landlords are those quota owners not reporting catch for any species during the year, and whose holdings at year's end are at least 100 kg less than they own.

Fishing Rights (SFRs)[9] following the finalization of the management plan in 1998, and so this trend may continue. The jump in 1998 is due to the new grenadier quota-holding clients mentioned above. The proportion of the catch now being leased out by those not reporting catch is getting to a level that might warrant some systematic monitoring of the situation and further investigation to determine how this might affect other stakeholders.

Another common concern related to landlording is the issue of quota ownership concentration. A danger of these two factors in combination is the potential for market power to develop in the hands of a few quota owners, such that they can exert control over vessel operators with regard to prices for fish and quota. Hogan *et al.* (1999) have shown ownership concentration in the SETF to be low as measured by the Herfindahl–Hirschman Index. The individual species indices are in a similar range to those for the New Zealand inshore fin-fishery, and an order of magnitude less than those for the New Zealand mid-depth species such as blue grenadier (Connor 2000). Neither quota landlording nor ownership concentration seem to be problems in the SETF. However, investigation of the fine structure of the industry may reveal localized market power developing in particular areas.

The Gap Hypothesis

As from 1993 (the second year of quota) a carry-forward provision applied in the SETF to assist in the inter-season balancing of catch against quota. In 1993 this was 10% of holdings, and in 1994 was increased to 20%. This creates a target band for an operator's total catch for each species at year's end, latterly between 80% and 120% of their quota holdings. This band represents a no-loss zone. As long as the quota holder's total reported catch is within this band, the over-catch or under-caught quota can be carried forward to the following season. For operators whose catch for the year lies outside this zone, the proportion of their holdings by which they miss the zone can be viewed as a measure of lack of success in maximizing their interests for that stock. We dub this proportion the 'Gap'.

We hypothesize that, under certain circumstances, a negative correlation should be apparent between the size of the Gap and the size of the quota holding to which it relates. Our reasoning is that, where asymmetries in transaction costs and information about the quota system exist, those with better information and lower costs of search and contracting for quota purchase or lease will find it easier to match their catch against quota. Our hypothesis is that, when ITQs are first introduced, such differences might be predicted by size of holdings; that is, that larger fishing businesses will have an initial advantage over smaller operators in knowledge about system rules, in obtaining information about quota availability, and in arranging transactions. We further hypothesize that this relationship should diminish over time as initial differences are reduced by learning, and as market signals drive both technical efficiency gains and reallocation of quota.

The expected correlation between holding size and ability to finish the season within the no-loss zone, and its progressive reduction, will also be dependent on a range of other factors that affect an operator's ability to both catch the fish and adjust quota holdings. This will mean that the relationship may be more apparent for some species than for others. For example, the ling species has a fully caught TAC, is targetable, fairly plentiful, and makes a good price. The key impediment to balancing for this species could be expected to be availability of quota. It is likely to take more search time and effort to locate quota in the market than for some other species, particularly when the system is new. If costs of this search are greater for smaller operators, as expected, they will be at a disadvantage in trying to balance their catch and quota, and this should show up as greater Gaps for small holdings. If economies of scale in harvesting pertain, the pattern may be exaggerated, as larger operations will be more able to afford the quota that is available, and smaller or less efficient fishers will find lease prices beyond their reach. A contrasting example is john dory which, due to its dispersed distribution, cannot be targeted but is of high value, and the TAC is more than double the usual catch. In this case there is a surplus of quota and it should not be difficult to locate. It should also trade for less than its use value because of the low probability that it will be fully caught. Small operators should find it easy to balance any over-catch of their holdings by leasing. However, large operators may need to carry large under-caught holdings in case catch ratios of the species are unexpectedly high.

For ling we might expect to see the Gaps of the smaller quota holders reduce over time as they establish wider contacts in, and knowledge of the quota market. They may adjust their fishing patterns or gear so that catch better reflects their holdings, and generally learn to better position themselves to end the year in the no-loss zone. Hence examination of trends and patterns in the relationship between the Gap and holding size may well provide an indication of the vitality of the quota system. If major impediments existed to market operation, we would not expect to see much change in the Gap to holding-size relationship. If we are to see the effect of the market, it

---

[9] SFRs are the statutory instrument for implementing ITQs, but they can only be granted once a Fishery Management Plan has been determined and approved by the Minister. While developing the SEF management plan, quotas have been implemented as conditions on permits. In conjunction with the limitation of new permits, this has restricted the ability of those other than fishing permit holders to own quota, although it has been possible.

should be apparent in a species such as ling more readily than in those subject to other constraints. However, extensions of Gap analysis for other species such as john dory may be able to offer policy insights for dealing with the issue of under-caught TACs. And finally, trends over time for intermediate species could give some assurance that the quota system is providing incentives that are driving behavioural change in fishing operations to maximize economic benefits within the overall constraints imposed by the TACs.

Gap analysis

We used ling to test the initial propositions above. Scatter plots for ling for the years 1992 and 1997 (Fig. 1) illustrate that a transformation in the distribution of Gaps has taken place over the period. The intervening years represent a gradual progression from one to the other. The 1992 plot shows a wide dispersion of points diminishing in an arrowhead formation as the size of holding increases. The 1992 vertical axis has been clipped for direct comparability with 1997, and several points are off scale, ranging up to 300% over-caught. This radical over-catch is reduced quickly in subsequent years, with only one client over 120% in 1997[10]. The change in distribution of points is clear. The large majority of clients for 1997 have achieved the no-loss zone, and points within the zone are spread across it from one bound to the other.

The results for ling support the suggestion that, in 1992, asymmetries existed in information, transaction costs, and/or operator efficiency for this species and the progressive reduction in the relationship between the Gap and holding size suggests that adjustment is taking place as the system matures. The fact that all except a handful of clients are able to balance their catch against holdings sufficiently to end the year in the no-loss zone is a clear indication that the quota system is working. Total catches are successfully constrained, while individual fishers with variable catches are able to adjust their fishing strategies and their holdings to maximize their interests within that constraint. The increasing proportion of ling quota that is leased each year supports the assertion that the quota market is instrumental in bringing about this result. In 1992, the volume of ling quota leased was equivalent to 42% of the total catch. In 1998 it was 75%. When other conditions in the fishery are favourable, the quota market in the SETF is able to work well to balance catch and quota.

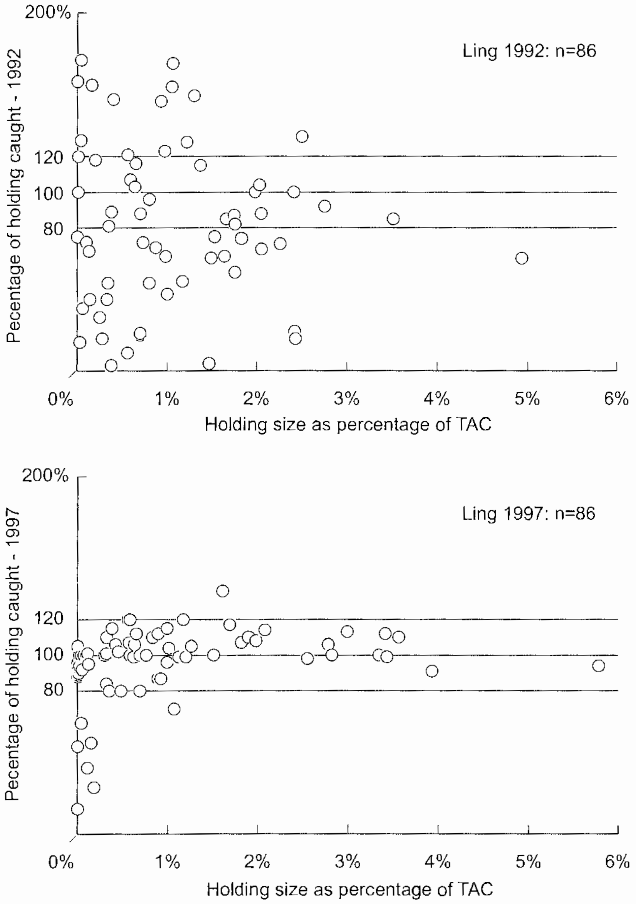


Fig. 1. Relationship between the proportion of holdings caught and holding size for ling, 1992 and 1997. Data for the largest quota owners have been grouped and averages used to protect client confidentiality. Data source: Australian Fisheries Management Authority.

Learning curves

Many of the other species in the SETF do not produce such clear patterns of adjustment. In general the less targetable species show more random distribution of the Gap when plotted, and do not seem by visual inspection to be changing markedly over time. To check this we assessed the Gap for each holding and averaged these across all those reporting catch. This average proportional deviation provides an index of system behaviour, or the stakeholders' ability to minimize quota losses, for which trends over time might be assessed. A zero average deviation would mean that all those reporting catch have caught >80% and <120% of their quota holdings.

The trends in the average deviations over time are quite consistent across species and provide an indication of what we term 'system learning'. The typical characteristic, for the years from 1992, has a negative slope between the first three points and then flattens out. The level at which it flattens out

---

[10] The management agency has been accommodating to operators who report over-catch, allowing retrospective balancing well into the following year for the first few years.

depends on the species but is very similar for a range of species. Learning curves for several SETF species are shown in Figs 2 and 3. John dory, mirror dory, flathead, morwong and redfish have all settled into the 20–30% range, although john dory shows greater volatility than the other species in the group. Ling demonstrates near complete success, with the index of <7% since 1995 and in 1997 it was 3%. The blue grenadier plot provides an indication of how large changes in the TAC level[11] can affect the curve, but also indicates the responsiveness of the system in turning the curve back down within a few years, despite no growth in the total catch. Another species in the same class as ling in 1998 is spotted warehou. The orange roughy stocks show mixed results, with the Eastern stock, which has been constrained tightly by the TAC, hardly registering any deviation in any year. The Western stock, on the other hand, has the most variable curve of all with high deviations fluctuating from year to year.

Of course, the value of the average deviation is going to depend to quite a high degree on the percentage of the TAC that is caught for the species. However, as the blue grenadier plot demonstrates, the curve can be affected strongly by strategies of quota holders even when the catch as a proportion of the TAC remains static. Our interpretation of the learning curves reinforces the earlier results. Stakeholders in the SETF have taken up the quota trading system and are using it with some vigour to maximize their interests. It has taken some years for the system to settle but by 1996, most of the learning curves had flattened out.

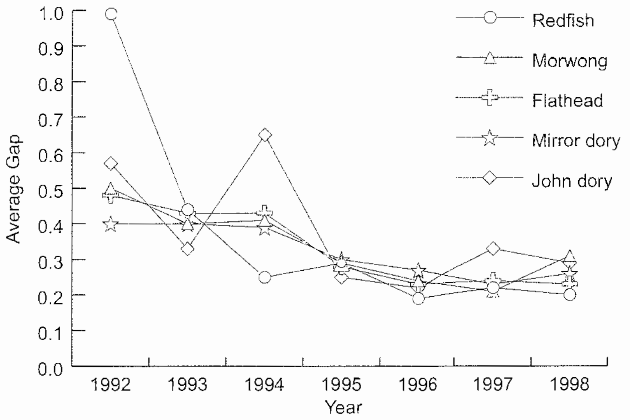


Fig. 2. System learning curves: average gap, over all participants, between end-of-year holdings level (±20%) and actual catches, for five SETF species, showing decline as management system matures. Data source: Australian Fisheries Management Authority.

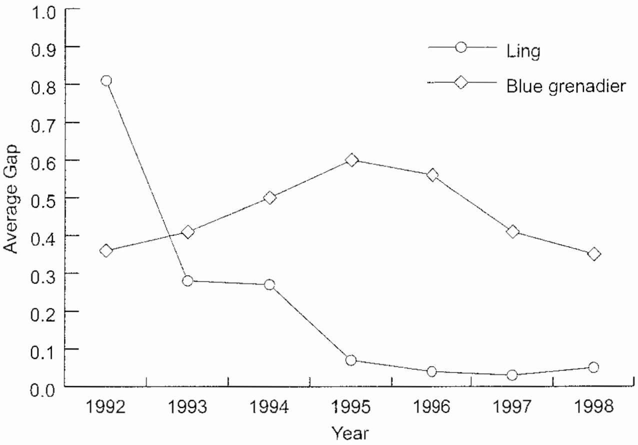


Fig. 3. System learning curves: exemplary (ling) and atypical (blue grenadier) characteristics. Data source: Australian Fisheries Management Authority.

Discussion and conclusions

Major institutional changes such as the introduction of new rights regimes into management systems take time to bed down. The SETF has had a rough start in many ways and, as has been pointed out by others (Squires *et al.* 1998), mixed trawl fisheries are not the ideal vehicles for demonstrating the virtues of ITQs. The specific conditions in the fishery, ecological, economic and social, make this even more complex and difficult to manage effectively than in other fisheries. However, the descriptive statistics and indicators presented in this study show that the quota market has contributed flexibility to the system. They show that it has assisted stakeholders to maximize their interests, given the constraints imposed by the TACs, the allocations of species mix, and the vicissitudes of the environment and the price of fish.

There are serious issues for research and management in the SETF that will not be solved by the market for quota. The significant fleet capacity reduction widely expected to be a result of the introduction of quota has not occurred, but this cannot be attributed to a failure of the management instrument or the quota market. This study has not assessed fleet change in the SETF beyond noting the relatively static number of vessels in the fishery, and the regulations restricting the number of vessel permits for the fishery limit any claim that ITQs have limited expansion of capacity. However, fishing strategies have changed because of quotas, away from efforts to catch more fish *per se*, toward maximizing the economic yield from a quota portfolio (Prince *et al.* 1999).

It is our view that the social and economic system in which the SETF is embedded plays a significant role in determining the rate of fleet adjustment, along with the age

---

[11] The allocated TAC more than doubled in 1994, whereas the TAC for the previous year was only 60% caught. Catch declined in 1994 and stayed below 1993 levels until 1997.

structure of the fleet and its operators. These factors interact with the institutional settings in complex ways. For example, the limited entry policy, besides creating a significant barrier to the entry of technical innovation to the fishery, may have created a disincentive for marginal fishers to exit through promoting an expectation that a SETF permit is a valuable asset. Where marginal fishers wishing to exit will only sell their permit as part of a whole business, including vessel and quota, they are unlikely to find many takers. Hence some may be hanging on, in the hope that quota prices will rise or that someone will eventually buy them out on their own terms.

However, given the effective use of output controls and the low opportunity costs of vessel capital, any expressed urgency regarding structural adjustment of the fleet must be regarded as unwarranted. If vessels are scrapped, the efficiency gains will be very small, and the social costs of loss of employment and local economic activity in regional coastal towns would not have to be large to tip the balance in favour of the status quo. On the other hand, the condition of effective output controls cannot be taken to be satisfied given the high percentage of discarding recorded in the fishery (Garvey 1998). Some modelling work has suggested that excess capacity locked into ITQ fisheries may exacerbate discarding and high-grading problems (Squires and Kirkley 1996). This implies that a well targeted capacity reduction program might help reduce the overall discard rate. The potential links between these issues in the SETF might be usefully investigated further.

Any reduction of uncertainty surrounding the condition of fish stocks and therefore the long-term stability of the TACs would assist stakeholders in making decisions about permanent transfers of quota assets, and possibly about exit. This will take time given the constraints on resources for research, but the lease market seems to be fulfilling a useful role in minimizing risks in the interim. It is clear that there is some inherent bias in the system against smaller operators in terms of the transaction costs of quota trading. This could be alleviated through a requirement to register prices for all quota transactions, and the monthly publication of average prices. AFMA could promote rationalization of small, unused quota holdings by offering owners a low- or no-cost facility to pool these and put them up for auction. Quota concentration and landlording do not seem to pose any immediate cause for concern in the SETF, but these are worth monitoring on a regular basis.

The final issue discussed here is that of the level of TACs relative to catch. The TACs for many species in the fishery are regularly under-caught by large percentages. Since 1992, landings have reached or exceeded the TAC for only six of the 19 stocks. In 1997, 13 stocks were less than 70% caught (Hogan *et al.* 1999). In some cases the high TACs are known to be justifiable on biological grounds, and in the case of blue grenadier may be driving economic developments. For many stocks this is not the case. Many TACs are above their highest historical catch levels and the biological status is uncertain (Tilzey 1999). The Gap analysis technique developed in this study makes clear the distributional effect of this situation. In general, a surplus of quota for which there will be no catch will have little lease market value. Those who catch the fish will be able to acquire quota to lease cheaply and capture rents that would otherwise pass to the quota owner in a more competitive market. In effect, the total rents from catching the stock, instead of being shared among the quota owners in proportion to their holdings, will be captured by those who happen to catch the fish. This distorts prices for lease, but also deflates prices for permanent trade. Add to this the uncertainty about future TAC decreases and it is little wonder that there is not more adjustment of permanent holdings. Some owners will feel their quota is worthless so they might as well stay in the fishery, rather than sell up.

This is a complex issue with too many 'unknowns' for any easy answer to apply. The multispecies 'mixed bag' nature of the fishery, the limited market for some species, the cost of increasing knowledge of the biological status of stocks, and high variability in environmental conditions and catchability of particular species, mean that analysis for practical policy action on these TAC levels will need to be detailed, systematic and multi-disciplinary. However, for some species, the above economic rationale, which extends to suggesting dropping TACs to levels that better reflect current catch levels, may warrant further investigation.

The exploration of quota ownership and trading, and catch data reported in this paper provide an innovative perspective on the dynamics of the SETF. Some with intimate knowledge of the fishery may find that the results here confirm their views; others may disagree and believe the approach to be simplistic. The study provides an optimistic view of the health of the SETF quota market, and our hope is that it can help to separate the question of whether the market mechanism is working, from the other issues of concern in the management of the SETF. Figures for recent years show that average returns to SETF fishing operations are increasing (Brown 1997; ABARE 2000). This could indicate a rebuilding of fortunes in the fishery as ITQ system learning progresses.

Acknowledgment

This paper originated in discussions between the authors and David Timcke, an economist then working for the Australian Bureau of Agricultural and Resource Economics. David was tragically killed in an accident before the study was fully developed, but we acknowledge his contribution to the early stages of this work.

References

ABARE (2000). Australian Fisheries Surveys Report 1999. (Australian Bureau of Agricultural and Resource Economics: Canberra.)

Arnason, R. (1993). Ocean fisheries management: recent international developments. *Marine Policy* **17**, 334–9.

Bjornland, H., and McKay, J. (1998). Factors affecting water prices in a rural water market: a South Australian experience. *Water Resources Research* **34**, 1563–70.

Brown, D. (1997). Australian Fisheries Surveys Report 1997. (Australian Bureau of Agricultural and Resource Economics: Canberra.)

Casey, K. E., Dewees, C. M., Turris, B. R., and Wilen, J. E. (1995). The effects of individual vessel quotas in the British Columbia halibut fishery. *Marine Resource Economics* **10**, 211–30.

Colby, B. G. (1995). Regulation, imperfect markets, and transaction costs: the elusive quest for efficiency in water allocation. In 'Handbook of Environmental Economics'. (Ed. D. W. Bromley.) pp. 476–502.

Connor, R. D. (2000). Trends in fishing capacity and aggregation of fishing rights in New Zealand under ITQs. In 'Use of Property Rights in Fisheries Management'. Proceedings of the FishRights99 Conference, Fremantle, Western Australia 11–19 November 1999. (Ed. R. Shotton.) FAO Fisheries Technical Paper No. 404/2, pp. 29–38. (FAO: Rome.)

Connor, R. D. (in press). Changes in fleet capacity and ownership of harvesting rights in New Zealand fisheries. (Marine Resources Service, FAO Fisheries Department: Rome.)

Conrad, J. M. (1995). Bioeconomic models of the fishery. In 'Handbook of Environmental Economics'. (Ed. D. W. Bromley.) pp. 405–32.

Copes, P. (1986). A critical review of the Individual Quota as a device in fisheries management. *Land Economics* **62**, 278–91.

Daly, H. E., and Cobb, J. (1994). For the common good: redirecting the economy toward community, the environment, and a sustainable future. (Beacon Press: Boston.)

Garvey, J. (1998). Interim integrated scientific monitoring program 1996 and 1997: end of project report to the Australian Fisheries Management Authority. (Bureau of Rural Sciences: Canberra.)

Gordon, H. S. (1954). The economic theory of a common-property resource: the fishery. *Journal of Political Economy* **62**, 124–42.

Grieve, C., and Richardson, G. (2001). Recent history of Australia's South East Fishery: a manager's perspective. *Marine and Freshwater Research* **52**, 377–86.

Hartwick, J. M., and Olewiler, N. D. (1998). The economics of natural resource use. (Addison–Wesley.)

Hogan, L., Thorpe, S., and Timcke, D. (1999). Tradable quotas in fisheries management: implications for Australia's south east fishery. ABARE report to the Fisheries Resources Research Fund. (Australian Bureau of Agricultural and Resource Economics: Canberra.)

ICES (1996). Report of the Study Group on the Management Performance of Individual Transferable Quota (ITQ) Systems. (International Council for the Exploration of the Sea: Copenhagen.)

May, R. M. (1976). Harvesting whale and fish populations. *Nature* **263**, 91–2.

Menz, K., Geen, G., and Collins, D. (1986). Issues in the management of the South-East Trawl Fishery. (Australian Government Publishing Service: Canberra.)

Moloney, D. G., and Pearse, P. H. (1979). Quantitative rights as an instrument for regulating commercial fisheries. *Journal of the Fisheries Research Board of Canada* **36**, 859–66.

NRC (1999). Sharing the fish: toward a national policy on Individual Fishing Quotas. Committee to review individual fishing quotas, Ocean Studies Board, Commission on Geosciences, Environment and Resources, National Research Council. (National Academy Press: Washington, DC.)

OECD (1993). The use of individual quotas in fisheries management. (Organisation for Economic Co-operation and Development: Paris.)

Prince, J., Baelde, P., and Wright, G. (1999). Synthesis of industry information on fishing patterns, technological change and the influence of oceanographic effects on fish stocks. Project No. 97/114. (Fisheries Research and Development Corporation: Canberra.)

Scott, A. (1955). The fishery: the objectives of sole ownership. *Journal of Political Economy* **63**, 116–24.

Smith, D. C., Smith, A. D. M., and Punt, A. E. (2001). Approach and process for stock assessment in the South East Fishery, Australia: a perspective. *Marine and Freshwater Research* **52**, 671–81.

Smith, S. A. Y. (1999). The Hunter River salinity trading scheme – ESD in practice. Second International River Management Symposium, Brisbane, Sept 30 – Oct 1, 1999.

Squires, D., Campbell, H. F., Cunningham, S., Dewees, C. M., Grafton, R. Q., Herrick, S. F., Kirkley, J., Pascoe, S., Salvanes, K., and Shallard, B. (1998). Individual transferable quotas in multispecies fisheries. *Marine Policy* **22**, 135–59.

Squires, D., and Kirkley, J. (1996). Individual transferable quotas in a multiproduct common property industry. *Canadian Journal of Economics* **29**, 318–42.

Terry, J. M. (1993). Individual transferable quotas for the fixed gear sablefish and halibut fisheries of Alaska. In 'The Use of Individual Quotas in Fisheries Management'. (Organisation for Economic Co-operation and Development: Paris.)

Tietenberg, T. (1995). Design lessons from existing air pollution control systems: the United States. In 'Property Rights in a Social and Ecological Context: Case Studies and Design Applications'. (Eds S. Hanna and M. Munasinghe.) (World Bank: Washington, DC.)

Tilzey, R. D. J. (ed.) (1999). The South East Fishery 1998. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Tilzey, R. D. J., and Chesson, J. (1997). South east fishery – quota species. In 'Fishery Status Reports 1997: Resource Assessments of Australian Commonwealth Fisheries'. (Eds A. Caton, K. McLoughlin and D. Staples.) (Bureau of Resource Sciences: Canberra.)

Tilzey, R. D. J., and Rowling, K. R. (2001). History of Australia's South East Fishery: a scientist's perspective. *Marine and Freshwater Research* **52**, 361–75.

Tullock, G. (1975). The transitional gains trap. *Bell Journal of Economics* **6**, 671–8.

Weninger, Q. R., and Just, R. E. (1997). An analysis of transition from limited entry to transferable quota: non-Marshallian principles for fisheries management. *Natural Resource Modeling* **10**, 53–83.

Manuscript received 15 November 1999; revised and accepted 9 August 2000

Mar. Freshwater Res., 2001, **52**, 399–410

Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition

N. L. Klaer

CSIRO Division of Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia
email: neil.klaer@marine.csiro.au

Abstract. Haul-by-haul steam trawler catch and effort data for 1918–23, 1937–43 and 1952–57, which cover a large portion of the history of steam trawling in the Australian South East Fishery, were examined in detail for the first time. There were 64 371 haul records in total. The catch-rate for all retained catch combined shows a strong decline overall, with a brief recovery during World War II, probably due to increased retention of previously discarded species. The fishing fleet moved to more distant fishing grounds and deeper waters as the catch-rate declined. The catch-rates of the main commercial species followed a similar pattern in a number of regions within the fishery. The catch-rate of the primary target species – tiger flathead (*Neoplatycephalus richardsoni*) – dropped considerably from the early, very high, catch-rates. Chinaman leatherjacket (*Nelusetta ayraudi*) and latchet (*Pterygotrigla polyommata*) – species that were apparently abundant in the early years of the fishery, virtually disappeared from catches in later years. The appearance of greater catches of jackass morwong (*Nemadactylus macropterus*), redfish (*Centroberyx affinis*) and shark/skate during the war and afterwards was probably due to increased retention of catches of these species. The disappearance of certain species from the catch may be due to high fishing pressure alone, or to a combination of fishing pressure, changes in the shelf habitat possibly caused by the trawl gear, and environmental fluctuations.

Extra keywords: fisheries management, south east trawl fishery, CPUE, historical, steam trawler, stock assessment.

Introduction

After early exploratory fishing, the South East Fishery (SEF) began in 1915, quickly becoming the main Australian fin-fish fishery. It has remained the primary supplier of fresh fish for the domestic market in the south-east region of Australia. The three steam trawlers initially imported by the New South Wales State Government used otter trawl gear, which is much like the gear used today by modern trawlers. The Government built more vessels and then privatized the fleet in 1923. Expansion continued until about 1929, by which time 17 steam trawlers were operating. Their numbers declined slowly to 14 vessels just before World War II.

Danish seine vessels began fishing in 1933, taking about 20% of the catch of the fishery up to the start of the war. When the Navy requisitioned fishing vessels during the war, both fishing effort and catch decreased. By 1943 only one steam trawler and a few Danish seine vessels were operating. Effort expanded immediately after the war, with 10–12 steam trawlers operating from 1946 to 1954, and the number of Danish seine vessels increasing until about 1965. After 1954 the steam trawlers began to disappear; the last steam trawler left the grounds in 1961.

Between 1961 and 1971 the fleet consisted only of Danish seine vessels (Tilzey 1994). Since the first modern diesel otter trawler entered the fishery in 1972, the number of Danish seine vessels has slowly declined to 30, whereas diesel trawlers increased up to 105 in 1991. The same year saw the introduction of an individual transferable quota (ITQ) system and, with the consolidation of quota holdings by multi-vessel operators, the number of vessels fishing decreased slightly (Tilzey 1994). The number of active trawlers has decreased since 1992 and fishing effort declined slightly in 1998 after increasing steadily from 1992 to 1997 (Tilzey 2000).

The fishery was primarily in shelf waters between 50 and 200 m depth. It targeted tiger flathead (*Neoplatycephalus richardsoni*), jackass morwong (*Nemadactylus macropterus*) and redfish (*Centroberyx affinis*) until the 1970s when the spawning run of gemfish (*Rexea solandri*) was discovered in slope waters between 300 and 400 m. The fishery expanded to greater depth in the 1980s to target blue grenadier (*Macruronus novaezelandiae*) and orange roughy (*Hoplostethus atlanticus*). The total annual landed catch of the fishery varied between ~1000 and 7500 t from 1918 to 1961, but rose to 62 269 t in 1990, mainly because of orange roughy catches.

10.1071/MF00101 1323-1650/01/040399

The current status of the fishery is outlined by Tilzey (2000). More than 100 commercial species are currently taken, and the long-term potential yield for most species is unknown. The 17 species subject to total allowable catch limits under the ITQ system account for more than 80% of the total catch. One species is considered to be overfished (gemfish), six are considered to be fully fished (jackass morwong, tiger flathead, redfish, ocean perch [*Helicolenus* spp.], blue warehou [*Seriolella brama*] and orange roughy) and one is considered to be underfished (blue grenadier). The status of the remaining species is uncertain.

This paper examines per-haul records of catches by steam trawlers in the period 1918–57, which covers most of the period that those vessels operated. Although the tonnage of the steam trawler vessels varied considerably, they all consistently used the same type of fishing gear, operated from the same home port area and used the same fishing routine. A fishing trip was generally about 4–6 days (Colefax 1934), and hauls of between ~3 and 5 hours' duration were made around the clock while on the fishing grounds (Roughley 1916; R. Mansfield, personal communication). A photograph of the *Moona*, one of the last steam trawlers to operate in the SEF, is shown in Fig. 1. Estimates of the total catch of the steam trawlers, the total catch of the trawl fishery and the number of steam trawlers that operated in most years are given in Table 1.

Fig. 1. Photograph of the steam trawler *Moona*, one of the last to operate in New South Wales waters. This vessel was formerly a mine sweeper in the New Zealand Navy, and fished from 1947 to 1958 for Red Funnel Trawlers Pty Ltd (R. Mansfield, personal communication).

Table 1. Estimated annual total commercial landed catch for the New South Wales South East Fishery fishery, the proportion of the total catch taken by steam trawlers and the number of steam trawlers operating each year

Includes a mixture of records by calendar and financial year. Total catch 1915–16 to 1947–48 from Fairbridge (1948) taking the greater of Marine Services Board or NSW State Fisheries Department annual catch statistics; total catch 1948–49 to 1952–53 from Houston (1954); total catch 1955–61 from best estimated total catch of flathead (includes some landings from Victoria), morwong and redfish combined plus 20% for additional species from Tilzey (1994); steam trawler catch 1915–16 to 1953–54 from Houston (1955); steam trawler catch 1955–58 from Red Funnel Trawler company landings in Klaer and Tilzey (1996); steam trawler catch 1960–61 from Red Funnel Trawler company vessel logbooks in Klaer and Tilzey (1996); no. steam trawlers working 1915–16 to 1953–54 from Houston (1955); no. steam trawlers working in 1955 from Blackburn (1978) given as 7.5 vessels in 1954–55; no. steam trawlers working in 1956–61 from Red Funnel Trawler company landings and vessel logbooks in Klaer and Tilzey (1996) and also in Blackburn (1978)

Year	Total catch (t)	Steam trawlers			Year	Total catch (t)	Steam trawlers		
		Catch	Vessels	% of total catch			Catch	Vessels	% of total catch
1915–16	740	740	3	100	1938–39	6391	5149	14	81
1916–17	743	743	3	100	1939–40	5619	3845	7–14	68
1917–18	861	861	3	100	1940–41	3648	1749	4	48
1918–19	1372	1372	3	100	1941–42	3113	961	3	31
1919–20	2533	2533	4–7	100	1942–43	1016	566	1	56
1920–21	2507	2507	7	100	1943–44	1032	488	1	47
1921–22	2452	2452	7	100	1944–45	4568	841	1–4	18
1922–23	1478	1478	7	100	1945–46	5802	1900	4–5	33
1923	1301	1301	–	100	1946–47	7360	3867	6–11	53
1924	2405	2405	5	100	1947–48	6885	4530	11–12	66
1925	3490	3490	5–8	100	1948–49	6419	4549	12	71
1926	3838	3838	9	100	1949–50	5857	3990	11–12	68
1927	4841	4841	10	100	1950–51	5094	3690	11	72
1928	5800	5800	11	100	1951–52	4767	3412	11	72
1929	6839	6665	17	97	1952–53	5571	3465	10	62
1930	6450	5884	16	91	1953–54	–	3541	10	–
1931	5187	5181	16	100	1955	4620	1407	6–8	30
1932	5325	4665	15	88	1956	3924	1240	4	32
1933	4410	4335	14	98	1957	4560	1064	4	23
1934	4493	4019	14	89	1958	3456	806	4	23
1935	4896	4433	13	91	1959	3228	–	2	–
1936	6275	4781	13	76	1960	3720	224	1	6
1937–38	6222	5129	14	82	1961	1296	12	1	1

All available per-haul steam trawler catch records were recently compiled into a single database (Klaer and Tilzey 1996). This data set makes it possible to compare catch-rates over a considerable period of the early development and expansion of the fishery. It also enables us to examine catch-rates in some detail by species, depth and area fished, that has never been possible previously. Steam trawler catch-rates have not been examined in detail since Blackburn (1978), who relied on earlier calculations made by Colefax (1934), Fairbridge (1948) and Houston (1955). None of these workers had the benefit of modern computers to arrange and analyse large data sets.

Methods

Data summary

Haul-by-haul steam trawler catch and effort data were available for the time periods 1918–23, 1937–43 and 1952–57. They totalled 64371 haul records. The data were converted to a standard format, the areas fished were geographically located, and the species codes interpreted by Klaer and Tilzey (1996). The cleaned haul-by-haul data have been used directly here. There are no haul-by-haul records available for the periods 1915–17, 1924–36, 1944–1951 and 1958–61.

Basic annual statistics were compiled from the data to show total hauls per vessel and year, as well as total catch, discarded catch (where recorded) and catch by primary commercial species landed.

To show spatial features of the data, regions within which to aggregate records had to be defined. As the early data, in particular, were not very accurately located (Klaer and Tilzey 1996), a suitable scale was considered to be broad fishing regions. The original records for 1918–23 contained latitude and longitude positions that were no more accurate than to approx. the nearest degree. Data for the periods 1937–43 and 1952–57 were only located according to grounds fished as shown as individual areas in Fig. 2, and it was sometimes not possible to decide to which adjacent grounds the records referred (Klaer and Tilzey 1996). The spatial grouping was therefore chosen as groups of identified adjacent fishing grounds to limit possible misplacement of records between spatial groups, while allowing for possible errors within groupings. Areas chosen that best grouped fishing grounds were separated by the following lines of latitude: 33.6°S, 33.2°S, 33.9°S, 34.5°S, 35.0°S, 35.6°S, 36.7°S, 37.6°S and 38.5°S. The defined areas were allocated identifying letters A–J (Fig. 2).

Mean catch-rate of all landed commercial species

There were 2918 hauls that had a value of zero for retained catch. To avoid the inclusion of trawls that were invalid because of gear failures in catch-rate calculations, those that had no retained catch were excluded, which left 61453 hauls for catch-rate analysis. This exclusion was supported by the 1918–23 records, which also recorded discarded catch. Of the 279 haul records in this time period with no retained catch, 268 also had no discarded catch.

Mean catch per unit effort (CPUE) was calculated by summing the total catch and dividing by the total number of hours trawled. The fishing procedure on steam trawlers seldom varied. The tow time of most trawls was recorded: 84% of these times were between 3 and 5 hours.

Catch-rate by main commercial species by area

Mean CPUE was calculated per species, calendar year and area as defined above, and results displayed for the most heavily fished regions that had a continuous history of fishing. An area and year were deemed to be sufficiently sampled when there were at least 200 hours of trawling (about 50 hauls) in a stratum. Only these results are presented to avoid spurious conclusions because of low sampling levels.

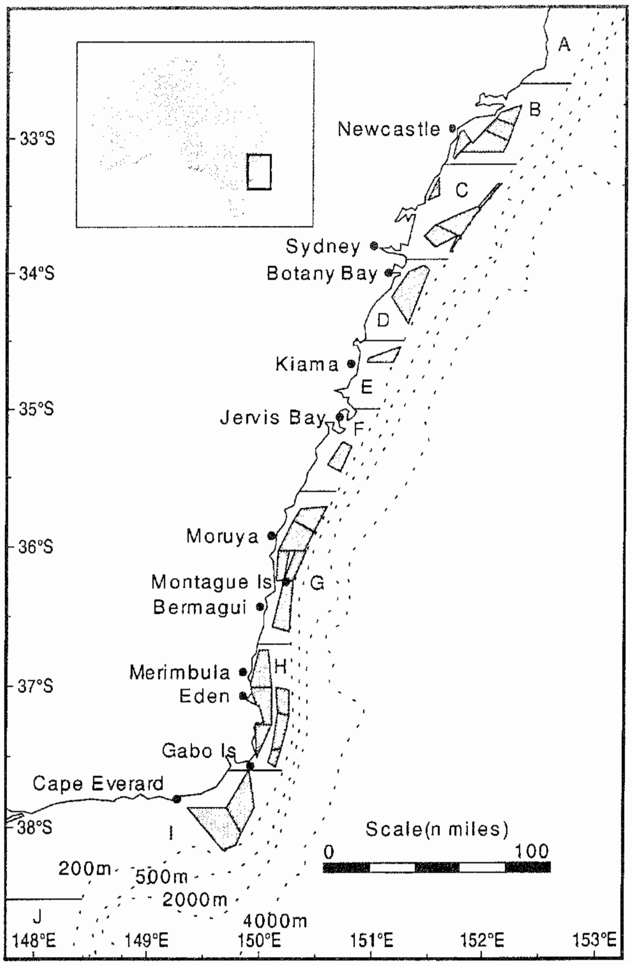


Fig. 2. Map of trawl grounds in shelf waters after Colefax (1934). The map also shows area divisions chosen for spatial aggregations used in this study.

As the depth fished may have a strong influence on the species composition of the catch, the percentage of hours trawled at different 20 m depth strata was also examined for these same areas for different periods in the fishery. Depth fished was given for 99% of records for the period 1918–23, 44% of records for 1937–43 and 92% of records for 1952–57 (Klaer and Tilzey 1996). For examination of patterns by depth fished, only records that had a recorded depth were included.

For area aggregations, it was important to allocate fishing effort as well as possible, to each of the broad fishing areas defined above. Hauls in the 1937–43 and 1952–57 data that were reported to have been made at the location coded as GABO (grounds associated with Gabo I.) were assumed to have been made in Area I, even though these hauls would be placed in area H using the latitude cutoff of 37.6°S; it is most likely that they actually occurred south of that line. Therefore, the 8797 hauls in these years that were reported to have been made in the Gabo I. Grounds were assigned to Area I.

The CPUE in catch-per-hour trawled by species was compared for the three areas that were most heavily fished over the history of the fishery: (1) the 'home' Area D off Botany Bay, (2) Area G around Montague I., and (3) Area H off Eden (see Fig. 2). Although Area I was heavily fished from 1943 onwards, it was not examined in detail because it provided no information over the 1918–23 period.

Species were encoded in the original records as two letter identifiers (Klaer and Tilzey 1996). There can be little doubt about the true identity of most of the species codes because of the small number of commercial target species, and published accounts of the composition of the steam trawler catches (e.g. Roughly 1916; Colefax 1934; Fairbridge 1948; Houston 1955; Blackburn 1978). It was not possible to separate shark and skate in the original records based on the two letter species codes, however (code 'SK' could be either), so that is why the combined category of shark and skate is used here. The leatherjacket was considered most likely to be chinaman leatherjacket (*Nelusetta ayraudi*) and latchet catches likely to be *Pterygotrigla polyommata* according to Klaer and Tilzey (1996) from examining Roughley's (1916) information about early trawl catches. Other leatherjacket species (F. Monacanthidae) may have been present, and some catch recorded as latchet was possibly red gurnard (*Chelidonichthys kumu*). The common names of latchet and gurnard were apparently used interchangeably at times in the commercial catch records, and the two fish are similar in appearance.

Results

Data summary

Estimates of the total catch of all landed fish taken from the SEF, the total landed catches of steam trawlers alone, and the number of steam trawlers operating for the entire history of steam trawling from 1915–61 are given in Table 1.

The number of hauls by vessel and year is given in Table 2. A large proportion of the total fleet is represented in the haul-by-haul data set for the periods covered. Some individual vessels made more than 1000 hauls in a year, as the *Bareamul* did during 1939 and 1940, an extraordinary number considering the time required for unloading and moving to and from the fishing grounds. Some of the vessels spanned the major periods of available data. The *Dureenbee*, for example, fished from 1919 to 1942. The demise of this vessel in 1942 was related by Loney (1993): 'A [Japanese] submarine attacked the trawler *Dureenbee*, 223 tons, on August 3, killing two seamen and a brother of the master, Captain Reid. Extensively damaged above the waterline by shell and machine gun fire, with her funnel shot away and all superstructure either smashed or burnt out, she drifted for several hours before going ashore one mile north of Moruya Heads'. Other vessels that spanned long periods of available data are the *Goolgwai* (28 years), *Goonambee* (22 years), *Goorangi* (21 years), *Korowa* (27 years), and *Mary Cam* (27 years).

Total annual retained catch by principal commercial species or species group is given in Table 3. The amount of catch discarded was also recorded for the very early period of the fishery, so those figures have also been shown. The records show that flathead, latchet and chinaman leatherjacket dominated early catches from 1918–23. Flathead was the main target species from 1937 to 43, with more morwong and redfish and much smaller catches of latchet and leatherjacket. During 1952–57, catches of morwong and redfish surpassed flathead catches, and catches of latchet and leatherjacket remained low. Catches of shark and skate were at a low level throughout; they were apparently seldom landed in 1923 and 1937–40. A relatively low and consistent catch of other species throughout shows that the main identified species were the primary commercial target species for the fishery, at least in terms of landed catch weight.

Mean catch-rate of all landed commercial species

A time series of CPUE values for the total landed catch of steam trawlers from 1924 to 1954 was produced by Houston

Table 2. Number of hauls by vessel and year

Covers most vessels operating during 1918–23, about half those operating in 1937–40, all vessels during 1941–43, about half from 1952–55 and most from 1956–57

Vessel	Year																			Total
	1918	19	20	21	22	23	37	38	39	40	41	42	43	52	53	54	55	56	57	
Alfie Cam							742	925	899	222					127					2915
Bareamul								793	1149	1042	829	675	226							4714
Beryl 2							839	908	685											2432
Brolga	541	507	216	626	603	108														2601
Dibbiu		158	132	544	639	15														1488
Dureenbee		91	174	397			947	892	1124	221	894	370								5110
Goolgwai							1	764	792					57	850	383				2847
Goonambee		208	198	620	462	46	893	940	984	194										4545
Goorangi		227	139	452	516	72	936	992	676											4010
Gunundaal	459	577		54	659	125														1874
Koraaga	729	506	225		607	111														2178
Korowa								668	817					768	791	401				3445
Maldanna														851	813	804	681	772	696	4617
Mary Cam							877	985	990	223	646	306			160					4187
Matong														691	824	802	895	697	792	4701
Moona														865	891	832	789	813	643	4833
Mulloka																	706	872	699	2277
Olive Cam							750	921	661											2332
Samuel Benbow									145	213										358

(1955), who based it in part on earlier work by Fairbridge (1948) and it is reproduced here as Fig. 3. The CPUE was calculated by dividing the annual total steam trawler landed catch by the total tonnage of steam trawlers that operated in the fishery each month, based on monthly returns to the Government Marine Services Board. Sections of the series that are comparable with periods where haul-by-haul data are available are shown in Fig. 4 as dashed lines. It is evident that the haul-by-haul calculation of steam trawler CPUE paints a very different picture to that of the catch per trawler-ton-month values.

The results of calculating haul-by-haul CPUE by dividing the total retained catch in each year by *(a)* total hauls, *(b)* total hauls that had a retained catch, *(c)* total hours fished and *(d)* total hours fished for those hauls with retained catch, all showed a pattern very similar to that shown in Fig. 4. It can be concluded, then, that the difference in the CPUE calculated here and that calculated earlier by Fairbridge (1948) and Houston (1955) is because the data sets and effort measures were different, rather than because of some property of the method used to calculate the mean CPUE. Fairbridge (1948) commented that he did not have haul-by-haul records for the period 1937–43 used here, and Houston (1955) makes no mention of such data. The haul-by-haul records were apparently extracted subsequently from company records that were not available to researchers at the time. The earlier CPUE series for 1915–16 to 1922–23 were calculated and presented in tabular form by Houston (1955), but were not presented as part of the graphical representation of the series as shown in Fig. 4 because he did not consider that catch-rates from the development period of the fishery would give a true representation of what fish were available.

The haul-by-haul picture of retained catch CPUE indicates a period of learning until about 1920 and then a levelling off. The CPUE by 1937 is less than 50% of the CPUE achieved in the early 1920s. From 1937 to 1940 the CPUE is reasonably steady, and then there is a clear increase of more than 50% in the CPUE from 1940 to 1943. By 1952 the CPUE had returned to levels comparable with those before the war, and it remained at about the same level to 1957.

The mean latitudes fished each year are shown in Fig. 5. Because the home port of the steam trawlers was Sydney or Newcastle for the entire time they operated, and these ports are at the northern end of the latitudinal range of the fishery, the mean latitude fished is also a good indicator of how far, on average, the trawlers travelled to the fishing grounds. In the years 1918–23, much of the fishing was in the grounds closer to the home ports, even though the southern grounds such as those near Eden were known and fished at times. Fishing appears to have occurred in more southern areas by 1937 and 1938, but to have then moved north again during the war, probably because of increased retention and even targeting of species that were previously discarded, and also the general risk to shipping. By 1952 the mean latitude fished was near the mean fished just before the war, and was even further south by 1954–57. The pattern of mean latitude fished has much in common with the mean CPUE in Fig. 4, indicating a movement further afield as CPUE declined.

The monthly mean latitude fished is given in Fig. 6, which shows a repeating seasonal movement, with northerly fishing at a peak in about October, and southerly in February. The seasonal movement was apparently strongest in 1952 and 1953, but weakened thereafter. Monthly mean latitude fished by month across all years is shown in Fig. 7, and the strong seasonal pattern is evident.

Table 3. Total number of hauls, hours trawled and catch per commercial species from SEF haul-by-haul records for the period 1918–57

Year	Hauls	Hours	Catch (t)								
			Retained	Discard	Flathead	Morwong	Redfish	Latchet	Leather-jacket	Shark/Skate	Other
1918	1749	6956	1010	177	578	14	1	192	103	59	65
1919	2313	9060	1858	236	992	0	2	337	282	119	131
1920	1108	3873	1136	215	486	1	4	192	375	29	51
1921	2768	10193	2326	434	1483	3	2	229	473	28	108
1922	3581	13511	3149	710	2113	0	2	215	682	18	124
1923	492	1858	443	113	311	0	0	22	104	0	6
1937	6470	21687	1950	–	1132	210	44	0	3	0	564
1938	9221	31893	3054	–	1943	322	40	80	55	1	617
1939	9326	33241	3064	–	1953	249	76	56	161	1	574
1940	2192	7921	731	–	410	36	22	22	67	1	174
1941	2416	8839	878	–	348	83	118	30	96	10	194
1942	1396	5222	617	–	186	28	130	21	92	73	87
1943	227	909	128	–	61	0	2	5	25	30	4
1952	3309	13356	1260	–	299	399	181	20	81	111	170
1953	4699	19015	1427	–	239	498	348	14	43	128	159
1954	3398	13611	1091	–	193	482	208	5	13	76	117
1955	3282	12763	1118	–	151	562	179	10	23	88	106
1956	3328	13559	1000	–	156	490	115	12	31	80	118
1957	3096	12757	846	–	79	433	105	20	15	85	5

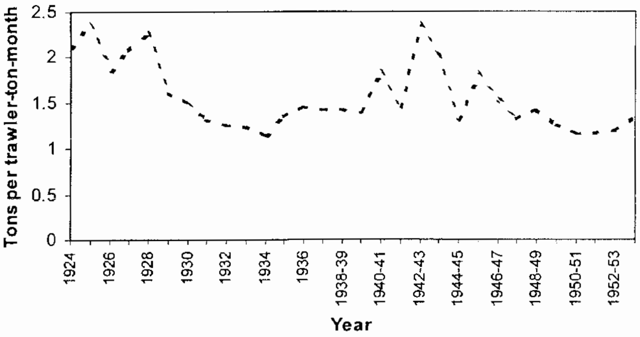


Fig. 3. CPUE for steam trawlers only for all landed catch (from Houston 1955).

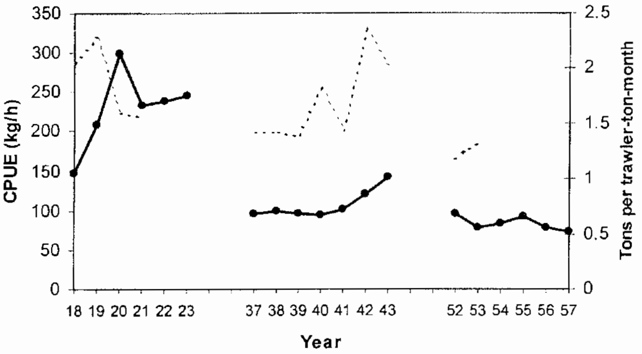


Fig. 4. CPUE for retained commercial catch by year. CPUE from haul-by-haul records in kg/h are shown as points on solid lines, and historical CPUE as presented by Houston (1955) in trawler-ton-months is shown as dashed lines. Note: Because of differences in the mode of reporting from calendar year to financial year, the 1918–19 data from Houston (1955) have been compared with 1918 calendar year data. Houston reported that the 1922–23 and 1923–24 data were incomplete, so data for those years do not appear here.

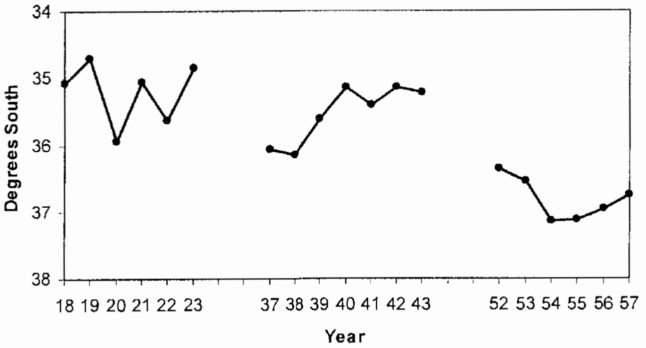


Fig. 5. Mean latitude fished by year. Note: The mean latitude fished does not necessarily indicate the actual position of the most heavily fished areas. Actual fishing in any year normally occurred in many areas within the range of about 30–40° south.

Mean depth fished each year is shown in Fig. 8. This shows that the vessels fished at depths averaging between 75 and 100 m from 1918 to 23, and between 110 and 130 m in 1937–42 and 1952–57. The overall pattern is again similar to that of the CPUE, indicating a movement to deeper water as CPUE declined.

Catch-rate by main commercial species by area

The proportion of hours fished in different areas each year is shown in Fig. 9. Only hauls that had position information (and a non-zero retained catch) were included, which was 44% of hauls ($n = 5279$) from 1918 to 1923, 95% of hauls from 1937 to 1943 ($n = 29746$) and 95% of hauls from 1952 to 57 ($n = 19965$).

In the period 1918–23, fishing was mainly confined to either Area D (the Botany Bay area near Sydney), or Area H (off Eden). There was a little fishing in Area C (north of Sydney) and Area G (around Montague I.). In most of these early years, the main fishing area was Area D.

In the period 1937–43 the fishing effort was much more evenly distributed over more regions, with the most hours trawled in Area I off Cape Everard. During the war there was less fishing far south of Eden and more in Areas D and F further north, particularly by 1943.

It appears that the most southerly areas of I (Cape Everard) and J (Babel I.) were discovered at some time between 1923 and 1937, a period for which there are no haul-by-haul data. By 1937, just less than half of the trawling was in these distant grounds.

During the period 1952–57, the areas fished remained relatively consistent throughout, with nearly half of the trawling directed at Areas I and J far to the south, as in the years before the war. Compared with the pre-war period, there was more fishing in Area H off Eden, and less fishing in Areas B, C, D, E and F closer to the home port. Area G around Montague I. was consistently fished at a low level throughout most years from 1918 to 1957.

The relative CPUE per species for Area D off Botany Bay is shown in Fig. 10. Very high catch-rates of more than 100 kg h^{-1} of flathead are shown in the period 1918 to 23. This corresponds well with Colefax's (1934) documentation of large catches of flathead in these years in the 'home' grounds. Catches in this early period also included considerable amounts of leatherjacket and latchet. The relative catch-rates per species remained reasonably constant between 1918 and 1923, with flathead contributing most to catch rates over that period, and then leatherjacket. The total CPUE was lowest in 1918 at about 150 kg h^{-1} and then fluctuated in the range of 180–290 kg h^{-1} from 1919 to 1923. By 1937, the catch-rate of all species combined was about one-third of the earlier levels. This was apparently due to a considerable reduction in the catch-rate of flathead, and much reduced catches of leatherjacket and latchet. During the period 1937–43, the flathead catch-rate did not recover

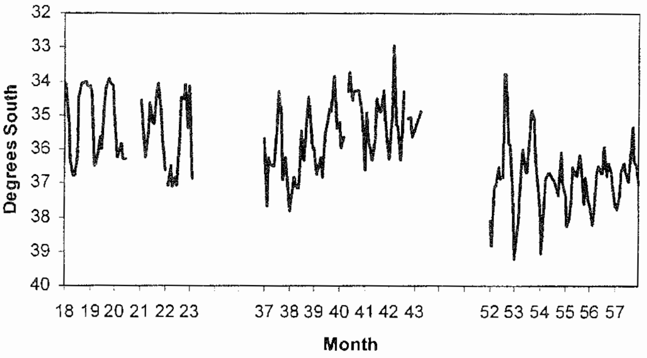


Fig. 6. Mean latitude fished by year and month.

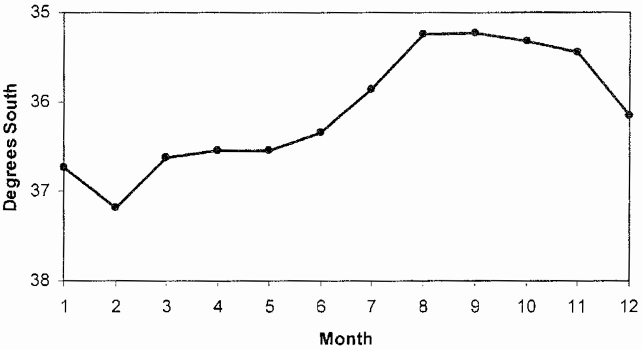


Fig. 7. Mean latitude fished by month.

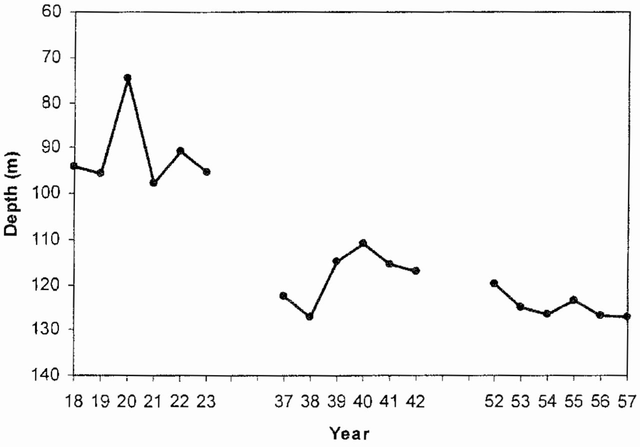


Fig. 8. Mean depth fished by year.

in this area, but the overall catch-rate increased because of increases in the catch-rates of leatherjacket and shark/skate, as well as the appearance of catches of redfish. The period 1952–57 shows the catch-rate of flathead declining to virtually nil, an initially higher catch-rate of redfish followed by a decline, and an appearance of morwong in the catches. There was a strong overall decline between 1918 and 1957 in the catch-rates of species that were apparently the primary targets in the early period of the fishery, namely flathead, leatherjacket and latchet. At the same time, the catch-rate of some species that were of minor importance during the early period, namely redfish and morwong, appears to have increased.

Area G around Montague I. shows a broadly similar pattern (Fig. 11) to that of Area D for the years in which there were enough hours of trawling to allow comparison. The early catch-rates for flathead were close to and possibly greater than, those in Area D, but the catch-rates of leatherjacket may have been smaller. Latchet also appeared in catches in Area D during this early period. Between 1937 and 1943 the overall catch-rate was sustained or even increased, apparently mostly due to an increased catch-rate of redfish. The overall catch-rates from 1952 to 57 were close to the pre-war level, and higher than that achieved in Area D. The relative catch-rate per species was similar to that of 1942, but much different to 1937, where redfish and morwong were scarcely represented.

Area H shows a similar pattern to Areas D and G, except perhaps that the overall catch-rate in 1918–23 was the highest of all areas, and that catch-rates of leatherjacket and latchet were comparatively higher in this area during that early period (Fig. 12). By 1937, CPUE for leatherjacket and latchet had dropped to low levels, flathead had declined by more than 50% and morwong had increased. Morwong were also taken at a low catch-rate in this area during 1918–23. Maintenance of the overall catch-rate from 1940 to 42 was apparently due to an increase in the catch-rate of redfish alone, in the same manner as Area G. By 1952 the overall catch-rate was about the same as for the 1937–42 period, but the catch-rate for flathead appears to have declined further, whereas the morwong catch-rate increased. The catch-rate per species was fairly stable from 1952 to 57.

From Fig. 8 we know that fishing was carried out in progressively deeper waters over the history of steam trawling. As fish species may have narrow depth distributions, it would be expected that a change in fishing depth would change the species composition of catches. To examine what difference a change in depth might make to the comparative catch-rate per species, histograms of the percentage of hours trawled at 20 m depth intervals for each time period and fishing area are shown in Figs 13–15. Fig. 13 shows that the vessels in the 1918–23 period fished mainly between 80 and 120 m, in 1952–57 between 120 and 160 m, and in 1937–43 at intermediate depths. Depths fished in Area G did not change much from 100 to 140 m throughout the years (Fig. 14). In Area H, there is a considerable difference between the depths fished in the early and late periods: mainly less than 80 m in 1918–23 and from 80 to 160 m in 1937–43 and 1952–57 (Fig.15).

CPUE by year per species for Area H in depths of less than 100 m is given in Fig. 16. For 1918–22 and 1937–39 the pattern is similar to that in Fig. 12. For the 1952–57

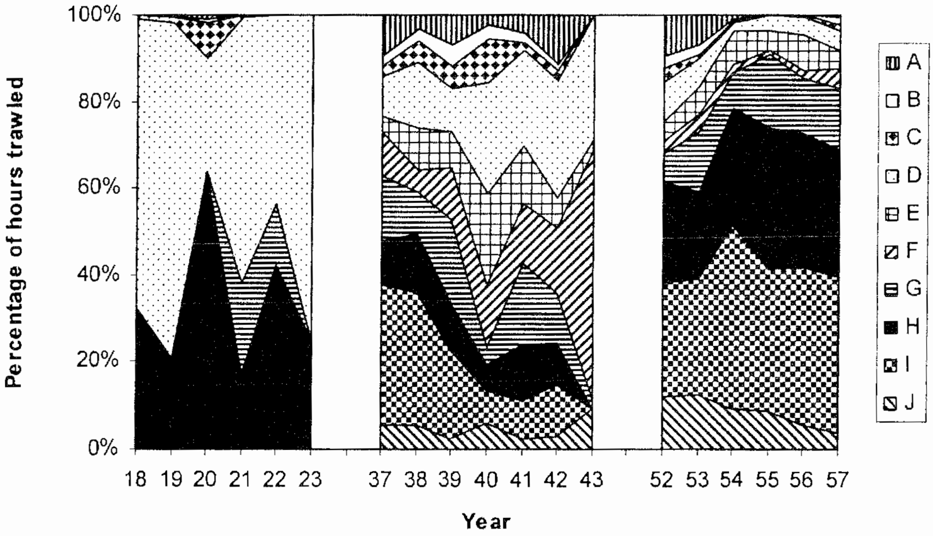


Fig. 9. Proportion of total hours trawled for hauls with location information that were made in each area.

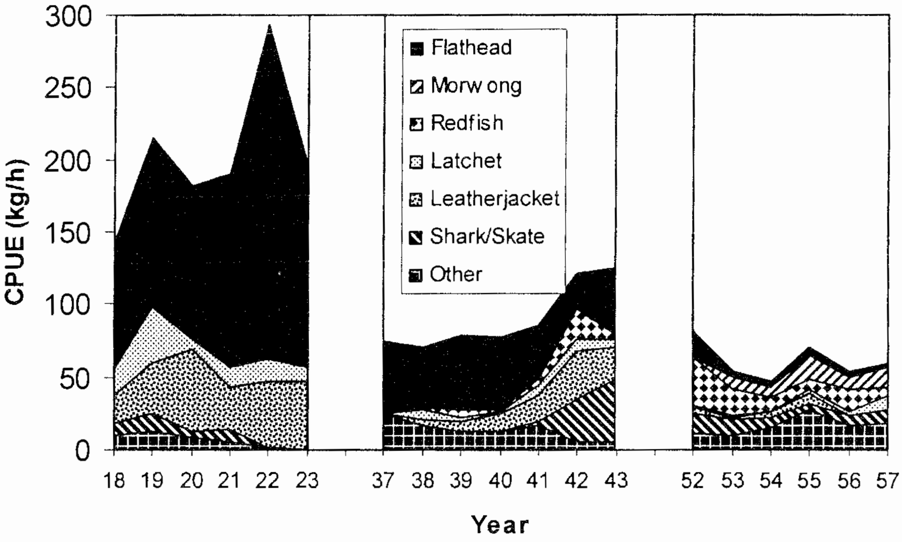


Fig. 10. Contribution per species to the total commercial CPUE by year for Area D.

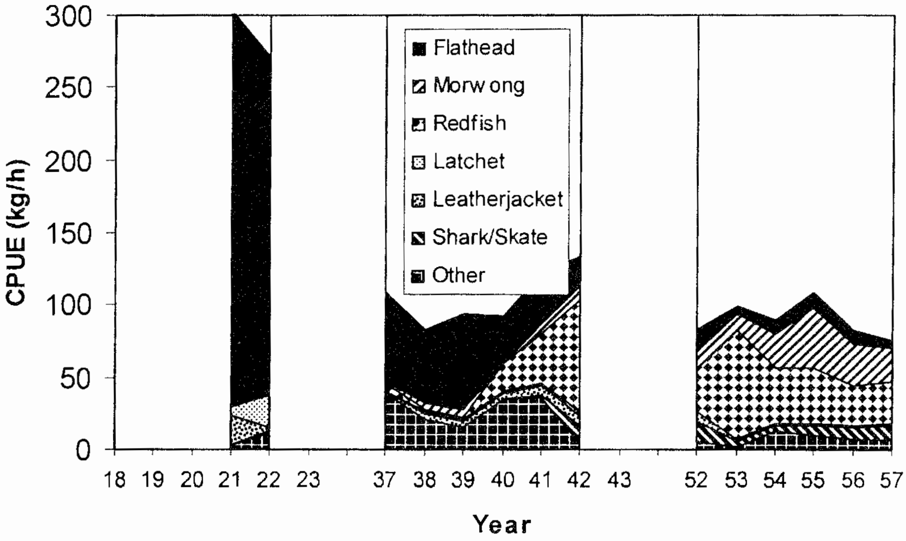


Fig. 11. Contribution per species to the total commercial CPUE by year for Area G.

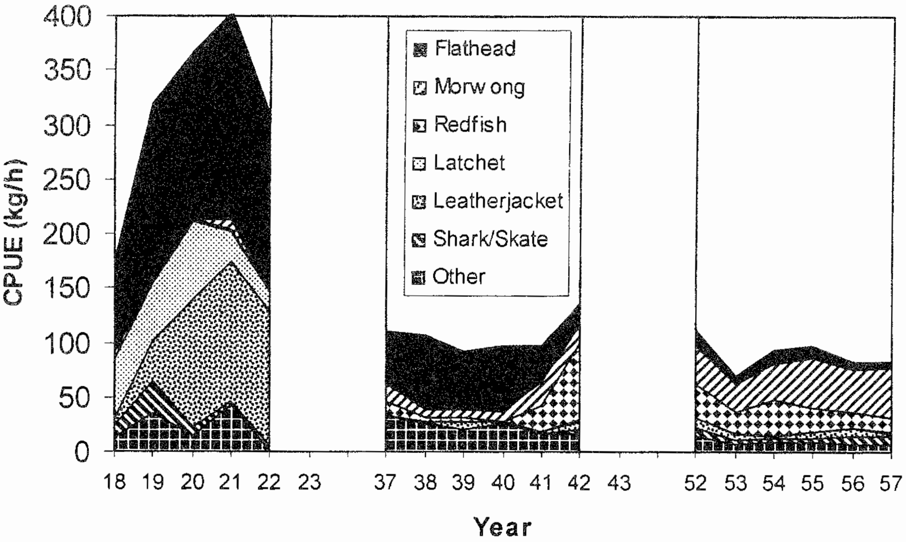


Fig. 12. Contribution per species to the total commercial CPUE by year for Area H.

period, the overall catch-rate is similar, but there is a difference in the pattern shown for redfish (which were almost absent), and a small increase in catch-rate of leatherjacket. Morwong was still strongly represented in the more shallow hauls of 1952–57. These results indicate that the appearance of redfish in catches after 1940 may be related to the increase in depth fished, and similarly, that some of the decline in the catch-rate of leatherjacket may perhaps also be attributed to the fishing depth change. However, change in depth fished does not seem to account for the increase in the morwong catch-rate.

Discussion

The overall trend in CPUE shows a decline over the history of steam trawling. There was certainly a period at the beginning of the fishery when the CPUE was probably lower than it could have been because of the inexperience of new crews, and a lack of knowledge about the fishing grounds and fish habits. Colefax (1934) said that 'there seems to have been an extraordinary variation in the efficiency of the different crews or gear, some vessels regularly returning with much higher catches than certain of the others, even though all were working over the same ground. In addition, considerable loss seems to have been experienced through the use of faulty equipment and the inability of the crews in certain cases to restore the latter to efficient working order'. In 1925 and 1926, a more efficient Vigneron-Dahl extension to the otter trawl gear was introduced. According to Hickling (1931), this increased the efficiency of the gear by one-third on average (Fairbridge 1948). There would have been many other changes to fishing practices, vessels or gear over the history of the steam trawling period that would have increased fishing efficiency. These changes, if they could be accounted for, would make the apparent long-term decline in the abundance of commercial species in the trawl grounds even greater.

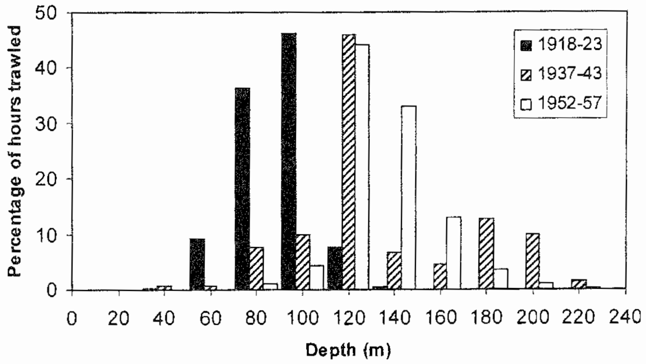


Fig. 13. Percentage of hours trawled by depth for the periods 1918–23, 1937–43 and 1952–57 in Area D.

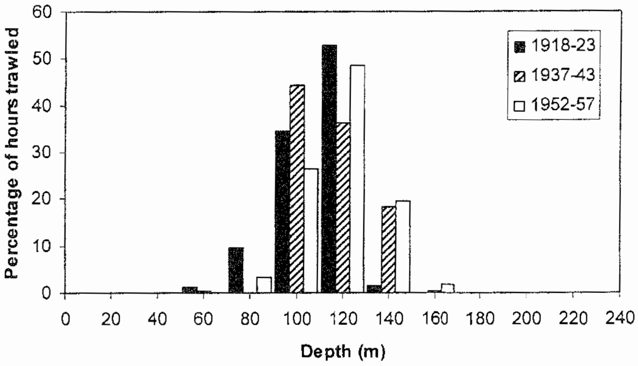


Fig. 14. Percentage of hours trawled by depth for the periods 1918–23, 1937–43 and 1952–57 in Area G.

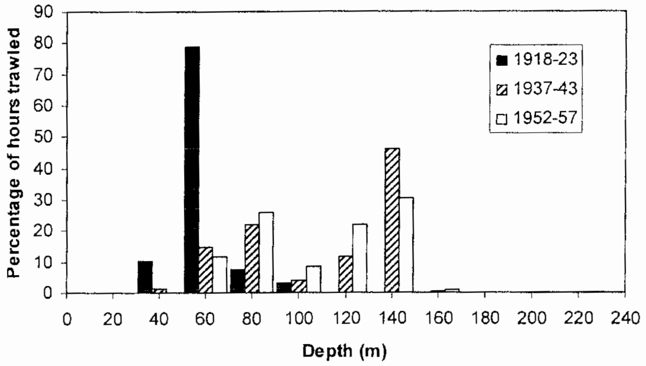


Fig. 15. Percentage of hours trawled by depth for the periods 1918–23, 1937–43 and 1952–57 in Area H.

There has been considerable examination of fisheries around the world, and also of the SEF (Fairbridge 1948), to determine how the large reduction in fishing effort during World War II changed catch rates. Observed changes in catch rate during this time have been used as an indicator of the state of the fishery in terms of exploitation in the years before the war. Haul-by-haul results here show that overall CPUE increased by 1943 by about 50% over pre-war levels. However, trends per principal target species show that much of the increase in the overall catch-rate from 1941 to 1943 is explained by an increase in catches of redfish and morwong.

Catch per trawler-ton-month in 1937–43 (Fig. 4) was of a similar order to 1918–21. However, the catch per hour trawled CPUE during 1937–43 was much lower than that of 1920–23. The new haul-by-haul data suggest that the fishery may have been heavily exploited just before World War II, and that there was apparently no recovery during the war (to 1943 at least) of the species mainly targeted before that time, flathead, leatherjacket and latchet.

Catch and catch-rates per species in the per-haul records refer to landed retained catch only. The interpretation of trends over long time periods may be complicated by changes in what species or size of fish were acceptable to the market at different times. For example, small sizes of certain species may become saleable, or when large catches are made, only larger, more valuable sizes might be retained. Fairbridge (1948) noted that the catches of flathead in the early period were probably representative of the true abundance of that species, but that some of the species that were marketable by 1948 were probably wasted earlier on. Morwong, redfish, latchet and barracouta became more acceptable through time. He also states that morwong was actively sought when flathead was 'off'. These changes in market acceptance could well explain the appearance of 'new' species in the catches as seen in Figs 10–12 and 16. The increase in shark/skate catch during the war years is apparent, as well as the much increased catch-rate of redfish and, to some extent, morwong. Redfish and morwong did not apparently appeal to the market in the 1918–23 period, as the figures in Table 3 also suggest. During the period 1952–57, fishing effort in the order of 3000 hauls caught about 600 tonnes of redfish and morwong. The total discarded catch in 1922 with 3581 hauls was 710 tonnes; it is therefore likely that a considerable portion of this discarded catch was redfish and morwong.

It is much more difficult to explain the disappearance of the early marketable species from the catches. Leatherjacket and latchet were, after flathead, the main targets in the early years of the fishery. Colefax (1934) says that leatherjacket figured prominently in catches in the Eden ground in these

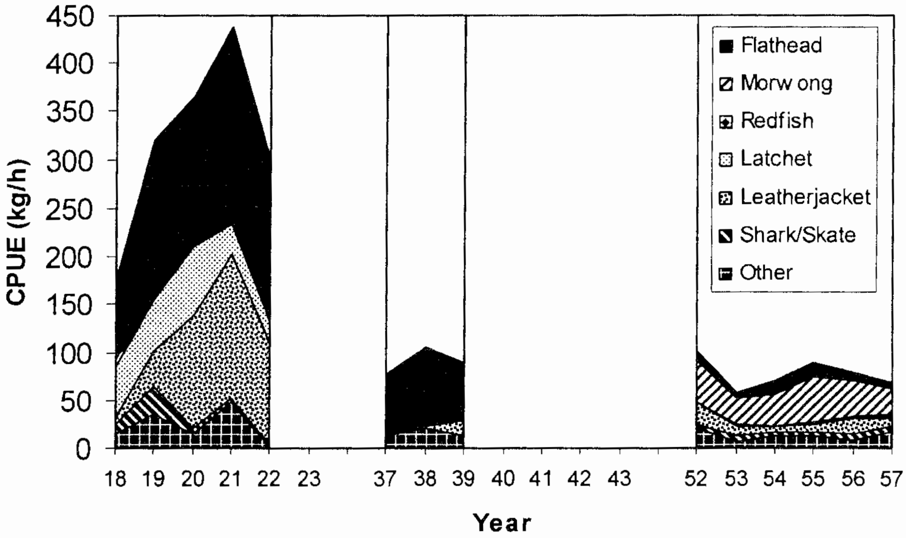


Fig. 16. Contribution per species to the total commercial CPUE by year for Area H in depths of less than 100 m. Note: Redfish CPUE has been included, but the values are small (<3 kg h^{-1} in all years) and do not clearly show at the scale of this figure.

years, almost to the total exclusion of flathead, and latchet were also taken in enormous quantities. He also noted that, in addition to the reduction in the flathead catch in later years, there was a corresponding reduction in the quantity of mixed fish (leatherjacket, latchet, john dory (*Zeus faber*), morwong etc.) taken. Although leatherjacket may be less likely to be caught in deeper waters, changes in areas and depth fished do not seem to be sufficient explanation for an apparently large decline in the abundance of leatherjacket, and also of latchet in the shelf trawl grounds of the SEF.

Changes in the abundance of flathead in particular have been well studied over the years, as this was the principal target species for the fishery, at least over the time when steam trawlers operated. The results here show that the fishing fleet moved further afield and into deeper waters as catch-rates declined. In some areas, the local depletion of flathead was much greater than indicated by aggregated catch-rates for the whole fishery. In the early period of good fishing in the Botany Bay ground (Area D; Fig. 10), the bulk of the catch was flathead that were 'very large and bursting with roe' Colefax (1934). The timing of the heavy fishing period was predictable from early September to early December, and vessels fishing then often returned to port with full holds well before the normal cruise time of 4–6 days. At the time, the heavy catch period was referred to as the 'Botany Glut'. This glut period became a yearly expectation, but failed to occur by 1926. By the 1930s, the Botany Bay ground was practically useless for trawling purposes, and was visited by boats only at the end of a trip (Colefax 1934).

It is clear that the overall catch-rate of flathead was sustained by the movement of vessels to new grounds or deeper waters. There were cases of localized, almost complete, depletion but there are no indications of cases of localized recovery of flathead catches.

There is little doubt that the abundance of the target species flathead, and possibly leatherjacket and latchet, was considerably decreased due to the heavy fishing effort on the shelf, to the point of over-exploitation in some years (Colefax 1934; Fairbridge 1948; Houston 1955). This in itself may explain apparent changes in the relative abundance of species in the catches over time, as each species has different biological characteristics that would result in different population responses to increased fishing mortality.

It is known that mobile fishing gear such as the otter trawl can change sea bed habitats (Auster *et al.* 1996). In heavily fished areas of the United States side of the Gulf of Maine, habitat complexity was reduced by direct removal of biogenic (e.g. sponges, hydrozoans, bryozoans, amphipod tubes, holothurians, shell aggregates) and sedimentary (e.g. sand waves, depressions) structures. Also, the removal of organisms that create structures, such as crabs and scallops, indirectly reduced habitat complexity (Auster *et al.* 1996). The physical effect is caused by the ground rope, chains and bobbins, sweeps, doors and any chaffing mats or parts of the net bag contacting the bottom (Jones 1992).

The first demonstrated link between habitat change and changes in trawl fish catch composition was for the Australian north-west shelf fishery, by Sainsbury (1987, 1988). Research trawl data showed that fauna associated with open sand benthos increased in the catch as the fishery developed, and that fauna associated with dense emergent benthos (e.g. sponges, gorgonians, alcyonarians) decreased. In other trawl fisheries such as the Spanish Galician shelf and slope, the abundance of non-commercial species has apparently increased as the abundance of primary commercial species has declined. These changes were attributed to fishing pressure and also environmental fluctuations affecting production in the region (Fariña *et al.* 1997).

The changes observed in the relative abundance of the principal commercial species on the SEF shelf during the steam-trawling period may therefore have various causes, some of which may not be easily reversed with a reduction in fishing. Theoretical models to explain the observed changes could be developed using additional information on species composition, bottom structure and sediments from recent scientific surveys in the region.

Acknowledgments

Mr Richard Mansfield, a former owner of Red Funnel Trawlers Pty Ltd (one of the main steam trawler companies operating in the SE Fishery), supplied company catch records that helped considerably with the interpretation of details in the per-haul data already held. He also helped with first-hand knowledge of operating procedures in the 1950s and early 1960s. Mr Norm Colless, who was an apprentice on the steam trawl vessels after World War II, also provided valuable information on the operating procedures of the vessels.

References

Auster, P. J., Malatesta, R. J., Langton, R. W., Watling, L., Valentine, P. C., Donaldson, C. L. S., Langton, E. W., Shepard, A. N. and Babb, I. G. (1996). The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): Implications for conservation of fish populations. *Reviews in Fisheries Science* **4**(2), 185–202.

Blackburn, M. (1978). Changes in size composition, indicative of stock conditions in the New South Wales trawl fishery, from 1945/46 to 1966/67. CSIRO Division of Fisheries and Oceanography Report No. 97.

Colefax, A. N. (1934). A preliminary investigation of the natural history of the tiger flathead (*Neoplatycephalus macrodon*) on the south-eastern Australian coast. *Proceedings, Linnean Society of New South Wales* **59**, 71–91.

Fairbridge, W. S. (1948). The effect of the war on the East Australian Trawl Fishery. *Journal of the Council for Scientific and Industrial Research* **21**(2), 75–98.

Fariña, A. C., Freire, J., and González-Gurriarán. (1997). Demersal fish assemblages in the Galician continental shelf and upper slope (NW Spain): Spatial structure and long-term changes. *Estuarine, Coastal and Shelf Science* **44**, 435–54.

Hickling, C. F. (1931). A comparison of the Vigneron-Dahl trawling gear with the steam otter trawl, in the hake fishery. *Journal du Conseil. Conseil Permanent International pour l'Exploration de la Mer* **6**, 421–31.

Houston, T. W. (1955). The New South Wales trawlfishery: review of past course and examination of present condition. *Australian Journal of Marine and Freshwater Research* **6**, 165–208.

Jones, J. B. (1992). Environmental impact of trawling on the seabed: a review. *New Zealand Journal of Marine and Freshwater Research* **26**, 59–67.

Klaer, N. L., and Tilzey, R. D. J. (1996). Catalogue and analysis of South East Fishery historic data. Final Report to the Australian Fisheries Research and Development Corporation. Project No. 90/023.

Loney, J. (1993). Wrecks on the New South Wales Coast. (Ocean Enterprises: Yarram, Victoria, Australia.)

Roughley, T. C. (1916). 'Fishes of Australia and their Technology.' (NSW Government Printer: Sydney.)

Sainsbury, K. J. (1987). Assessment and management of the demersal fishery on the continental shelf of northwestern Australia. In: 'Tropical Snappers and Groupers: Biology and Fisheries Management'. (Eds J. J. Polovina and S. Ralston.) pp. 465–503. (Westview Press: Boulder, CO.)

Sainsbury, K. J. (1988). The ecological basis of multispecies fisheries, and management of a demersal fishery in tropical Australia. In: 'Fish Population Dynamics'. 2nd Edn. (Ed. J. A. Gulland.) pp. 349–82 (John Wiley: Chichester.)

Tilzey, R. D. J. (1994). The South East Fishery – a scientific review with particular reference to quota management. (Australian Government Publishing Service: Canberra.)

Tilzey, R. (2000). South East Fishery – quota species. In 'Fishery Status Reports 1999: Resource Assessments of Australian Commonwealth Fisheries'. (Eds A. Caton and K. McLoughlin.) pp. 119–141. (Bureau of Rural Sciences: Canberra.)

Manuscript received 1 August 2000; revised and accepted 11 September 2000

Mar. Freshwater Res., 2001, **52**, 411–17

Fishers' description of changes in fishing gear and fishing practices in the Australian South East Trawl Fishery

Pascale Baelde

Division of Science and Design, School of Resource, Environment and Heritage Sciences, University of Canberra, ACT 2601, Australia

Abstract. Between the mid 1980s and early 1990s, the concurrence of three major events significantly altered the structure and dynamics of the demersal trawl sector in the Australian South-East Fishery (SEF). These events included marked technological improvement, severe decline of major fish stocks and introduction of an Individual Transferable Quota system. They have led to a switch from maximizing catch volume to maximizing catch composition and quotas, with important associated changes in fishing practices and catches. To better understand these changes and their effect on stock assessment and management, an industry survey asked SEF trawl fishers to describe their fishing gear and fishing practices in detail. This paper is a qualitative synthesis of current trends in fishing that most significantly affect the single-species, logbook-dependent assessment and management of the fishery. It demonstrates how effective collaboration between scientists and fishers can benefit fisheries research and management, by helping scientists make more informed analysis and interpretations of fisheries data.

Extra keywords: industry information, multi-species fishery, ITQ management.

Introduction

Fisheries systems are in constant evolution, in biological, technological and management terms, with significant changes in fishing gear and fishing practices. It is necessary to have a good understanding of these changes to properly assess and manage fisheries. This is particularly important in the case the Australian South-East Fishery (SEF), for which stock assessment and management rely essentially on fisheries-dependent data and interpretation of trends in commercial catch rate (Tilzey 1999). However, scientists generally have only a limited practical knowledge of fishing gear characteristics and of the many factors that influence fishing behaviour and fishing success. The need to improve collaboration between them and the fishing industry is increasingly recognized in fisheries sciences (e.g. Hilborn 1992; Hilborn and Walters 1992).

This paper is a qualitative synthesis of fishers' description of their fishing gear and fishing practices in the trawl sector of the SEF. It focuses on the factors that most significantly affect, and potentially undermine, the current assessment and management processes in the SEF. The influences of market demand and quota management on fishing practices, as described by fishers, are also discussed.

The SEF is one of Australia's oldest commercial fishery and currently supplies the bulk of the demand for fresh fish on the domestic market (Tilzey 1999). It is a multi-gear, multi-species fishery the historical development of which has been marked by successive decline of exploited stocks and discovery of new resources (Tilzey 1994). There are several subfisheries within the SEF, including two demersal trawl fisheries, the 'market fishery' and the offshore orange roughy (*Hoplostethus atlanticus*) fishery, the non-trawl fishery and the Danish-seine fishery. This paper is concerned with the market fishery, which occurs from the shallow depths of the continental shelf down to the shelf break and continental slope, to depths of ~500 m.

After the failure of early input management measures, an Individual Transferable Quota (ITQ) management system was implemented in 1992, covering the 16 most important species in the fishery.

Methods

The study took place in 1997 and began with a series of pilot interviews from which a questionnaire was developed for subsequent in-depth interviews. Face to face, semi-structured interviews were then conducted using the questionnaire as a guide to ensure that the same topics would be addressed with each respondent. The interviews were designed to assess the effect on fishing behaviour of modern navigational and fishing aids (Global Positioning System (GPS) and plotters) and changes in net design, and also the effect of market demand and quota management. Much care was taken to keep the interviews flexible, extending the discussion beyond purely scientific concepts (Johannes *et al.* 2000). Beside specific and practical questions, the questionnaire included open questions to give fishers an opportunity to expand in the directions they wished to. Reliability checks (which verify the consistency of answers to related questions) were also built in the questionnaire by using methods described in Beed and Stimson (1985) and Lyberg *et al.* (1997).

10.1071/MF99149 1323-1650/01/040411

All major fishing ports in the SEF were visited over a two-month period, with the aim of interviewing as many active, full-time skippers as possible. By the end of the survey, the majority (33) of them had been interviewed, all but two of the skippers who were approached agreeing to contribute to the interviews. More detailed information on the survey methodology and outcomes is available from Baelde (1998).

Results

Between the mid 1980s and early 1990s, three major and more or less concomitant events profoundly transformed the structure and dynamics of the fishery. These events were the development of new fishing technology, the severe decline of the major species (gemfish, *Rexea solandri*) sustaining the fishery at the time, and the implementation of an ITQ management system.

Evolution of fishing technology

GPS-plotters. SEF fishers started using the GPS progressively from the mid 1980s, at a time when it was operational for only a few hours a day. By the early 1990s the GPS was fully operational and the majority of fishers had acquired one. The GPS is now usually combined with plotters. GPS-plotters have increased fishing efficiency by increasing the accuracy of navigation and net setting on the fishing grounds. The GPS allows the continuous and exact positioning of a boat over a fishing spot, and the plotter allows the electronic recording of the exact locations of trawl shots and any ground features of interest (e.g. hook-ups). Most fishers agreed that GPS-plotters have become essential to fishing.

Demersal trawling initially developed in the 1970s on 'clear' and safe muddy grounds to target gemfish aggregations. As the abundance of the gemfish stock declined, GPS-plotters helped fishers extend their fishing towards rougher but more productive grounds, mostly around the continental shelf break and upper slope. Fishers can now target a variety of species by manoeuvring their trawl fishing gear closer along reefs, without damaging the nets.

Another important benefit for fishers of the accuracy of GPS-plotters is that they waste less time during fishing operations. Before the GPS, to locate precisely a fishing spot and shoot the gear over it, fishers used radars, landmarks and echo sounders (to follow depth contours) in combination. This required great skills and knowledge of local grounds and was time consuming, especially under difficult weather or current conditions.

Net design. When board trawling first started in the SEF, fishers designed nets specifically for catching gemfish on soft grounds. Fitted with chains, they were built to fish hard on the sea floor, at low speed, with a wide and low net opening (~3–4 m high) and long wings to herd the fish. They were big nets capable of handling large quantities of fish ('bulk fishing').

As the fishery expanded to harder grounds on the shelf break/upper slope, new nets were designed that fishers refer to as 'multi-purpose' nets or 'high-lift' nets. High-lift nets are small and made of lighter and stronger material compared with earlier nets. They have a high opening (~5–6 m high), short (or 'cut-away') wings and bigger mesh size, and are fitted with rubber disks (6–14 inches). With their reduced ground contact, they can be towed over several types of grounds, including rough areas, at fairly fast speeds. They are designed to catch a variety of species (e.g. blue and silver warehous, *Seriolla brama* and *Seriolla punctata*; redfish, *Centroberyx affinis*; silver trevally, *Pseudocaranx dentex*) during their spawning runs in winter months.

Some fishers also use a secondary type of nets, which they refer to as 'scratch' nets. These nets have kept some of the characteristics of the gemfish nets, although they are smaller and have a slightly higher headline and are fitted with small rubber disks. They are designed to catch species more dispersed and closer to the sea floor (e.g. flathead, *Neoplatycephalus* spp. and *Platycephalus* spp.; ling, *Genypterus blacodes*; ocean perch, *Helicolenus* spp.; various species of sharks), which are usually not caught with high-lift nets.

'Scratching' usually refers to fishing at times when catches are expected to be poor, i.e. during night time or in summer. Scratching shots are generally long shots, up to 7–8 h, compared with ~3 h on average for high-lift shots.

Boat horsepower. Since the quota management was implemented in 1992, about one-third of interviewed fishers have up-graded the horsepower of their boats, by between 20% and 50% of the original power. The use of high-lift nets was invoked as one of the major reasons for increasing horsepower, because of their high opening and fast towing speed.

General fishing strategies

Between the mid 1980s and early 1990s, bulk fishing practices for single species catches were replaced with fishing for more diversified species. This type of fishing initially developed after the decline of the gemfish stock, and was later further promoted with the implementation of an ITQ management system. Fishers now focus on catching smaller quantities of mixed species, and on spreading their catches throughout the year, to benefit from smaller landing sizes/better market prices and to maximize their quotas.

The 'mixed-bag'. Beside using multi-purpose high-lift nets, fishers are developing several other ways to diversify their catches. Some target depths or grounds where the distributions of several species are known to overlap, others prefer to trawl over a wide range of depths during a single shot, or simply increase the length of a tow. Also, with the help of the GPS, some fishers finish a tow over the edges of canyons or gutters to 'pick up' some species known to inhabit this particular type of habitat (e.g. blue eye trevalla, *Hyperoglyphe antarctica*; ling). However, the most common way described by fishers to catch a mix of species is to fish on different grounds known to carry different suites of species.

Timing of fishing. A large part of demersal trawling in the SEF is governed by a strong diel pattern, which is particularly marked between the shelf break and upper slope in winter. Fishers make, on average, 2–3 shots during daylight but the first shot, or 'morning shot', is regarded by market fishers as the most productive one and the one not to be missed.

The diel cycle is driven by the migration of the 'feed layer', presumably a mixture of macroplankton and various species of fish, concentrating in a horizontal band ~200 m deep. This feed layer is believed to be a major source of food for commercial finfish species and to regulate their migration, on and off the sea floor daily, and in and out of fishing grounds seasonally. The importance of similar diel patterns to fishing dynamics has been shown in other trawl fisheries (Dorn 1998). As a general rule, during winter months, the feed layer moves down to the sea floor at daybreak, associated with concentrations of various species (the species composition depending on the area). It is essential for successful fishing to set the trawl nets accurately on the fishing spots at the time when the feed layer goes down.

Around midday, the feed layer goes back up again in the water column, and the fish appear to disperse, with declining catches. At the end of the day, just before dark, fishing tends to improve again during what fishers call the 'dark shot'. The feed layer is much reduced in summer and market fishing slows down markedly at that time of the year.

'Targeting', 'speculating' and 'running away'. Market fishing is typically speculative because the species distribution on the fishing grounds is never totally predictable. Most commercial species have a wide depth distribution and tend to mix with each other, and fish aggregations also tend to be very mobile and to move between grounds. Fishers need to constantly re-locate fish aggregations.

A few species can be specifically targeted (e.g. blue grenadier, *Macruronus novaezelandiaea*; redfish; blue eye trevalla), on some grounds and at some times, when their dense aggregations form identifiable fish marks on echo sounders. However, most fishers agree that to identify market species, or even distinguish fish marks from the feed layer, is generally frustrating guesswork. They usually see no clear relation between what they see on their echo sounders and the composition or size of their catches. Thus, they tend to spend little time, if any, searching for the feed layer or fish marks before fishing. For the morning shot, most fishers go straight to a spot, which they have chosen the day before.

When market fishing, fishers do not target the fish themselves, but rather target a small piece of ground where a suite of species is expected to be caught. They know approximately what catches to expect on a particular ground at a particular time from previous fishing experience and knowledge of local grounds. However, they can never be totally sure of what the fish are doing and they do get surprises at times. Some accidental catches are welcomed, whereas others are not.

Fishers described how the practice of 'running away' from fish aggregations is increasing in the SEF, in order to avoid unwanted species (and sometimes limit discarding). They are learning to avoid some species by avoiding particular depths or particular grounds. However, they also pointed out that they can only steam away from 'already caught fish': it is recent fishing experience on a ground, their own or someone else's, that best informs fishers of what species are likely to be caught on that ground.

Information exchange between fishers. To plan their next fishing operation, fishers need to maintain day-to-day information, not only on fish availability on the fishing grounds (to reduce speculation on catches), but also on the size and composition of other fishers' recent catches (to predict market demand). Although a few fishers (usually the most skilled ones) rely solely on their own fishing experience, many fishers continuously 'fish for information'. In the case of these fishers, communication with other fishers significantly influences their fishing patterns. Communication was greatly facilitated when mobile phones replaced radios because it allowed more private exchange of information with selected fishers.

Fishers described how, within a fishing season, fishing patterns are governed by short (from a few days to a few weeks) cycles of resource 'depletion/dispersal' through fishing and 'renewal/aggregation' through fish migration back onto the fishing grounds. Catches are always better on a 'fresh' ground, i.e. which has not been fished for some time. Every fisher tries to be first on these grounds by keeping informed on where other fishers have worked recently.

Variation in fishing strategies within the SEF fleet

The fishing strategies described above are not uniformly adopted within the SEF fleet. Fishing behaviour depends on a large part on fishers' economic imperatives and operational structure. Today, there are, roughly speaking, two major business categories participating in market fishing.

The two business categories in the market fishery. In the mid-1980s, high concentrations of the deep-water orange roughy were discovered. Unfounded optimism about the size and productivity of the stock resulted in high investment in this offshore fishery (Pascoe 1993) and, with government incentives, a fleet of purpose-built large vessels was rapidly established. After being initially very high, catches then declined dramatically and the fleet of 'orange roughy boats' switched to market fishing. This resulted in the distinction of the 'family' type of business and the 'company' type of business.

Family businesses are run by fishers who operate small to average size boats (between just below and just above 20 m in length) during daily trips at sea. They usually own and skipper their boats and have relatively small quota holdings. Company businesses usually have large quota holdings attached to several larger boats (between 20 and 30 m) that are skippered by mostly hired skippers, or sometimes business partners. Skippers' skills have become a tradeable commodity and it is quite common for hired skippers to change boats within or between companies.

Influence on fishing patterns. With their larger quotas, company skippers are usually less constrained in their fishing activities and the need to maximize quotas is not as crucial for them as it is for other operators with smaller quotas. However, owners of larger boats have to pay higher running costs and higher quota fees and often put pressure on their skippers to catch large quantities of fish (bulk fishing). They can still offset low market prices with large landings, and also some of them have their own fish processing factories.

Small boat operators concentrate their fishing activities during periods of highest productivity (i.e. daytime in winter), whereas company skippers tend to fish 24 h each day, all year round, and in all weather conditions. While at sea for several days, they keep fishing throughout the night, usually making 1–2 long 'scratch' shots on shallow grounds on the continental shelf or deep grounds on the continental slope (below 500 m). Non-quota species (e.g. various species of sharks) are particularly being targeted during these operations.

Discussion

In theory, ITQ systems are expected to eliminate much of the incentive for the race to catch fish, to reduce fishing effort as fishers switch from maximizing quantity to maximizing quality, and to improve the economic efficiency of fisheries (e.g. Munro and Pitcher 1996; Dewees 1998). Experience in the SEF is quite different.

The race is still on

The quota regime has transformed the nature of competition between fishers but the race is still on. Although bulk fishing practices have significantly been reduced (although this is still practiced to some extent by company boats), catching a 'mix-bag' that matches both quota holdings and market demand is still proving difficult for many fishers. Most interviewed fishers complained of the added hardship that quota management has imposed on them, referring in particular to the 'inefficient' ways they have to fish today.

Economic studies conducted by ABARE (Australian Bureau of Agriculture and Resource Economics, Canberra) have shown that, whereas there have been short-term improvements in the economic efficiency of the fishery just after the implementation of the quota system, the longer term trends are not so promising (Tilzey 1999).

Increase in fishing effort

The overall number of active trawl boats in the SEF has declined by about 23% since the introduction of quotas, mostly through a government funded adjustment scheme (Tilzey 1999). However, there has been a re-distribution of some of the remaining boats between the orange roughy fishery and the market fishery. The number of boats participating in the latter fishery has in fact increased from 55 in 1990–91 to 64 in 1995–96 (Hogan *et al.* 1998; in Tilzey 1999).

The number of hours trawled, which was relatively stable between 1986 and 1991, has consistently increased since the early 1990s, increasing by 34% from 1991 to 1997. During the same period, total quota allocation for all species combined (excluding orange roughy) has increased by 81%, and total landings have increased by 16% (Tilzey 1999). The relentless fishing activity of company boats probably contributes significantly to this increase. This is considered as a major failure of the quota management in the SEF, especially when considering that part of this effort is targeted at non-quota species. Similar shift in fishing effort towards non-quota species has been observed in other ITQ managed fisheries (e.g. Burke *et al.* 1994) and it was long predicted in the SEF (Tilzey 1994).

Effect of GPS-plotters

The effect of GPS-plotters on fishing power has recently been analysed in the Australian Northern Prawn Fishery (NPF) by Robins *et al.* (1998). The results of this study suggested that GPS-plotters could increased the fishing power of the entire trawl fleet by 12%, after every fisher had used them for at least three years (to take into account a necessary learning period in effectively using these electronic aids). The effect of GPS-plotters was reflected in an increase in the effectiveness of each unit of nominal fishing effort (fishing day in this case).

However, fishing motives in the NPF are quite straightforward compared with fishing motives in the SEF. The NPF is a highly targeted fishery (the above-mentioned study focussed on target fishing for one species of prawn) and under no output control. In this fishery, GPS-plotters allow fishers to repeatedly shoot their nets on a productive area until catches decline; further, the extra time saved from being more accurate on the grounds is used to increase fishing (Robins *et al.* 1998).

In the SEF, the expectation that improved technology should increase single species catch rate would only be true for some species in some circumstances. Fishers' motives and the definition of 'fishing efficiency' itself differ totally in this multi-species fishery under output controls. By contrast to fishers in the NPF (Robins *et al.* 1998), SEF fishers find it actually difficult to estimate the percentage increase in their catches or catch rate since using GPS-plotters. One of the fishers' most frequent comments was that, by making fishing easier and more accurate, GPS-plotters in fact give them the greater flexibility they need at sea to catch a 'mix-bag'.

For example, even though GPS-plotters have likely increased fishing efficiency during the morning shot, fishers tend not to shoot the gear again, and move to another ground. This has probably much to do with the strong diel pattern that drives the productivity of market fishing. But also, even when fishers would have enough time to shoot the nets again before the fish disperse, they tend not to repeat a shot on a same ground to maximize their quotas ('running away').

Mismatch between quota holdings and actual catches

Making the right business decision on what to catch, where and when has become an essential part of 'fishing skills' in the SEF. The species-mix demanded on the market, the species-mix of quota holdings, and the species-mix available on the fishing grounds do not always match. As observed in other fisheries (Alverton *et al.* 1994; Gillis *et al.* 1995; Annala 1996), SEF fishers maintain that one consequence of the ITQ management system has been increasing discarding practices. The generally small size of single species ITQs increases the likelihood of quickly over-catching some species and can seriously limit the efficiency of fishing operations. Also, the lack of flexibility in the SEF quota system can bring the fishing fleet to a crisis point when an unpredictable increase in abundance and distribution range occurs for one species, as was recently the case for blue warehou.

The situation was worsened in the SEF by the fact that the quota system was implemented at a time when the fishery had entered a period of dramatic transformations of its structure and dynamics (still ongoing today). These transformations also led to some changes in catch composition. However, ITQ packages were at the time allocated to fishers mostly on the basis of their historical catches, and as a result they do not match well the composition of today's catches. Against expectations, the trading of quota between fishers has been fairly inefficient and few fishers have managed to re-adjust their initial quota holdings to their catch patterns today. The small sizes of fishers' initial quotas have limited their financial ability to engage in quota trading (Tilzey 1999).

But the situation is improving

As should be expected, a learning period is necessary for an industry to adapt their fishing practices and business skills to the major changes in management regime that an ITQ system represents. There are positive signs that fishers in the SEF are just coming out of a long 7-year learning period. The strong and systematic opposition from many fishers to the quota system is progressively diminishing as they are gaining more experience with this system.

The reduction of by-catches and discards is one of the greatest challenges in fisheries' assessment and management. Various approaches are being used to resolve these difficult problems, including evaluation of discard rate through catch monitoring programmes at sea and development of more selective fishing methods. Industry is also increasingly being invited to contribute to these programmes.

The developing practices of 'running away' from unwanted catches also have the potential to reduce discarding. Whereas some fishers still regard such practices as frustrating limitations to their operations, others accept them as an integral part of fishing today. However, 'running away' does not simply equate with 'not fishing', it requires new operational as well as business skills. In New Zealand too it is expected that discarding practices will be reduced as fishers gain more experience with the quota system (Annala 1996).

As in many fisheries, communication between fishers plays an important role in fishing strategies (Allen and McGlade 1986). In the SEF, the exchange of information between fishers seems to have increased since the quota system has led to more transparency in fishers' activities. Better communication is helping fishers to adapt their fishing to the quota regime more efficiently; it reduces the uncertainty of speculative trawling and contributes to limit discarding.

Stock assessment strategies

It is well recognized that using commercial catch statistics recorded in logbooks can give a misleading picture of the status of fish stocks (e.g. Hilborn and Walters 1992). However, logbooks represent the most comprehensive coverage of the SEF and they are, and will remain for some time, the major source of information for resource assessment and management in this fishery. Their value could be greatly improved if used in conjunction with industry information. For example, the important changes in electronic equipment and net design such as those described in the present study are not taken into account in SEF stock assessment mostly because scientists are unaware of them.

The limitations of the classical single species approach to the assessment and management of multi-species fisheries are well recognized and, in the SEF, are also a continuous source of contention between scientists and fishers. The industry information gathered during this study shows how some fishing practices have the potential to selectively drive down the catch rate of some species, with no relation to change in their abundance. These include the increase in fishing activity during less productive periods (e.g. at night-time and during summer), the stretching of fishing activities outside the normal fishing season (i.e. at a time when fish aggregations disperse), and the practices of 'running away' from fish aggregations (i.e. from potentially good catches).

Scientists are now paying more attention to using species composition as an index of the status of 'multi-species stocks' (e.g. Gabriel 1996; Biseau 1998). In the SEF, preliminary analysis of the species composition (quota species) of landings indicates that the average daily 'species richness' (S) and 'species diversity' (H) of these landings have both steadily increased since the early 1990s (Larcombe 2000). Also, these two indices exhibit much less pronounced winter–summer seasonal trends. These results clearly reflect the changes in fishing practices towards diversifying catches.

The more holistic approaches to scientific stock assessment and management that are currently developing, i.e. harvest and management strategy models (e.g. Smith *et al.* 1999), are also more promising. These models use decision-making processes to incorporate uncertainty in stock assessment and better integrate fishing behaviour (Hilborn 1992; Smith *et al.* 1999). To properly develop such models requires effective industry participation. As pointed out by Smith *et al.* (1999), these new trends in research and management fit better with the co-management approach progressively adopted and legislated by Australian management agencies.

The success of this study is mostly due to the fishers' high participation rate in the survey and their willingness to volunteer information on their fishing practices. It clearly shows the benefit that can be gained from collaborative work between scientists and fishers.

As already stated by others (e.g. Hilborn 1985), the study of fishers should be a major part of fisheries research. Too few studies (e.g. Dorn 1998) give consideration to factors such as fishers' socio-economic needs in analysing fisheries, despite the major influence that these factors have on fishing decision and associated catches. Until we seriously look into this, our poor understanding of fishing strategies will continue to undermine the validity of scientific assessment and limit the effectiveness of management.

Acknowledgments

I thank all the fishers who so generously contributed their time and expertise to this study. I also thank Jeremy Prince and Guy Wright for their comments and advice at the start of the work, and Kevin Rowling, Richard Tilzey and Robert Johannes for their helpful comments and suggestions on an earlier draft. This study was funded by the Fisheries Research and Development Corporation (Project No 97/114).

References

Allen, P. M., and McGlade, J. M. (1986). Dynamics of discovery and exploitation: the case of the Scotian Shelf Groundfish Fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1187–200.

Alverton, D. L., Freeberg, M. H., Murawski, S. A., and Pope, J. G. (1994). A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper No 339.

Annala, J. H. (1996). New Zealand's ITQ system: have the first eight years been a success or a failure? In 'Individual Transferable Quota'. (Eds G. R. Munro and T. J. Pitcher.) *Reviews in Fish Biology and Fisheries* (special issue) **6**(1), 43–62.

Baelde, P. (1998). Synthesis of industry information on fishing practices and their effects on catch rate analysis (bottom trawl sector) In 'Synthesis of industry information on fishing patterns, technological change and the influence of oceanographic effects on SEF fish stocks'. (Eds J. Prince, P. Baelde and G. Wright.) FRDC Project No. 97/114, Canberra, Australia. 70 pp., appendices.

Beed, T. W, and Stimson, R. J. (Eds) (1985). 'Survey Interviewing: Theory and Techniques.' (Allen and Unwin: Sydney.) 224 pp.

Biseau, A. (1998). Definition of a directed fishing effort in a mixed species trawl fishery, and its impact on stock assessments. *Aquatic Living Resources* **11**(3), 119–36.

Burke, L., Annand, C., Brander, R. B. L., Etter M. A., Liew , D., O'Boyle, R., and Peacock, G. (1994). The Scotia–Fundy inshore dragger fleet ITQ program. Background, implementation, and results to date. ICES Council Meeting Papers, (ICES: Copenhagen.) 10 pp.

Dewees, C. M. (1998). Effects of individual quota systems on New Zealand and Bristish Columbia fisheries. *Ecological Applications* **8**(1), supplement, 133–8

Dorn, M. W. (1998). Fine-scale fishing strategies of factory trawlers in a midwater trawl fishery for Pacific hake (*Merluccius productus*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 180–98.

Gabriel, W. L. (1996). The role of targeted species in identification of technological interactions in Mid-Atlantic Bight groundfish fisheries. *Journal of Northwest Atlantic Fisheries Science* **19**, 11–20.

Gillis, D. M., Peterman, R. M., and Pikitch, E. K. (1995). Implications of trip regulations for high-grading: a model of the behavior of fishermen. *Canadian Journal of Fisheries and Aquatic Sciences* **52(2)**, 402–15.

Hilborn, R. (1985). Fleet dynamics and individual variation: why some fishers catch more than others. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 2–13.

Hilborn, R. (1992). Current and future trends in fisheries stock assessment and management. *South African Journal of Marine Sciences* **12**, 975–88.

Hilborn, R., and Walters, C. J. (1992). Quantitative fisheries stock assessment: choice, dynamics and uncertainty. (Chapman & Hall: New York.)

Hogan, L., Thorpe, S., and Timcke, D. (1998). Issues in individual transferable quotas in Commonwealth fisheries. In 'Outlook 98, Proceedings of the National Agricultural and Resources Outlook Conference, Canberra, 3–5 February 1988, vol. 1, Commodity Markets and Resource Management'. (Australian Bureau of Agricultural and Resource Economics: Canberra.)

Johannes, R. E., Freeman, M. M. R., and Hamilton, H. J. (2000). Marine biologists miss the boat by ignoring fishers' knowledge. *Fish and Fisheries* **1**, 257–71.

Larcombe, J. W. P. (2000). Fleet dynamics and the use of catch rate data in the South East Fishery, Trawl Sector. Fisheries Resources and Research Fund, Research Report, Canberra.

Lyberg, L., Biemer, P., Collins, M., de Leeuw, E., Dippo, C., Scwartz, N., and Trewin, D. (1997). 'Survey Measurement and Process Quality.' [Wiley Series in Probability and Statistics.] (J. Wiley: New York.) 777 pp.

Munro, G. R., and Pitcher, T. J. (Eds) (1996). Individual Transferable Quota. *Reviews in Fish Biology and Fisheries* (special issue) **6**(1), 116 pp.

Pascoe, S. (1993). ITQs in the Australian South East Fishery. *Marine Resource Economics* **8**, 395–401.

Robins, C. M., Wang, Y-G., and Die D. (1998). The impact of global positioning systems and plotters on fishing power in the northern prawn fishery, Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1645–51.

Smith, A. D., Sainsbury, K. J., and Stevens, R. A. (1999). Implementing effective fisheries management systems – an Australian partnership approach. *ICES Journal of Marine Research* **56**, 967–79.

Tilzey, R. D. J. (Ed.) (1994). The South East Fishery – a scientific review with reference to quota management. (Australian Government Publishing Services: Canberra.)

Tilzey, R. D. J. (Ed.) (1999). The South East Fishery 1998. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Manuscript received 3 November 1999; revised and accepted 19 September 2000

Mar. Freshwater Res., 2001, **52**, 419–30

Trawl operations in the South East Fishery, Australia: spatial distribution and intensity

James W. P. Larcombe, Kevin J. McLoughlin and Richard D. J. Tilzey

Bureau of Rural Sciences, PO Box E11, Kingston, ACT 2604, Australia

Abstract. Trawl areas and intensities were mapped at coarse (22 km 1986–99) and fine (1 km 1995–99) scales, and statistics reported by area and depth stratum. Total effort in hours was relatively stable to 1992, then increased substantially to 1999. The total distance trawled from fine-scale analysis showed a similar trend for the 1995–99 period. Coarse-scale analysis from 1986–99 indicated effort increases in north-east Bass Strait in particular, and also off western Tasmania and west of Bass Strait. There was little change in the total area of the fishery from 1995 to 1999, but grid cells on the periphery showed considerable interannual variation in the presence or absence of fishing. Increased or redistributed effort tended to further concentrate in the relatively small high-effort areas, rather than increasing equally across the grounds, or spreading to new grounds. In the total management area, a small proportion of the 1 km grids was fished. However, in 200–1000 m depth strata, ≥50% of the grids were fished with some intensity. The consequences and compromises of spatial scale are discussed in terms of data quality, the use of trawl effort as a surrogate for marine disturbance, and the interpretation of catch rates.

Introduction

The South East Fishery (SEF) extends around south-eastern Australia, from Barrenjoey Point, New South Wales, to Cape Jervis, South Australia, and out to the 200 nmile Exclusive Economic Zone (EEZ). The SEF trawl fishery is managed by Total Allowable Catches (TACs) for 15 species (or species-groups) of fish and one crustacean, introduced over 1988–92, and allocated to fishers as Individual Transferable Quotas (ITQs). There are additional input controls including restrictions on gear, vessel entry and vessel size (see Grieve and Richardson 2001). Before 1992, >100 SEF otter trawlers were active in any one year, but the widespread introduction of ITQ management was followed by a decline in the number of active vessels to 85 in 1998. Although the SEF fleet contains a significant number of Danish seiners (18 active vessels in 1998), the fishing activities of these vessels are not described here. In 1998 the reported landed trawl and Danish-seine catch was ~28 000 t. Catches comprise a wide range of taxa, but are dominated by comparatively few commercial species (Klaer and Tilzey 1994). The total SEF area is 1.27 million km^2. However, much of this area lies outside the 1000 m isobath and is rarely fished.

This study was initially prompted by the need to examine fishing activity within the waters around south-eastern Australia to assess possible marine disturbance. As a result of the Australian Federal Government's *Oceans Policy* (1998), these waters are the subject of a multiple-use regional marine planning process. An interim ecosystem-based classification of Australia's marine and coastal environments (Interim Marine and Coastal Regionalisation for Australia; IMCRA Technical Group 1998) serves as a starting point for this process. In the absence of independent data, fishing effort is increasingly being used as a factor to which ecosystem changes can be related (Greenstreet and Hall 1996; Greenstreet *et al.* 1999) or as an 'indicator' of marine disturbance (Ward *et al.* 1998). Within this setting, a thorough and quantitative understanding of how fishing effort is distributed over space and time is essential (Greenstreet *et al.* 1999). Such an understanding is also important in interpreting and standardizing catch rates derived from the fishery and in the design of industry-dependent and independent surveys, to assist the SEF stock assessment process.

Trawlers in the SEF have been required to maintain a detailed log of operations and catches since October 1985. This study provides a detailed picture of the spatial distribution and intensity of otter trawl operations within the SEF, and examines changes over time. This was achieved through the simple production of maps, as well as quantitative analysis of fishing effort over spatial scales, depths and intensities. The work also develops and explores methods for analysing fishing effort within a spatial framework.

10.1071/MF99169 1323-1650/01/040419

Methods

Data

The SEF logbook data are referred to as the SEF1 database and contain information on start and end position for each trawl operation (shot), estimated landings by major species per shot and very limited details of the trawl gear. Port landing weights of quota species have also been closely monitored since 1992 as part of the ITQ management system, but the data in this SEF2 database cannot be allocated to a particular shot or location. The SEF1 database includes operational data from both Danish seine and 'conventional' trawl. Trawl data only are the subject of this work. Trawlers use a variety of net configurations and dimensions including broad, low mouthed designs termed 'scratch nets' and taller designs termed 'high-lift nets' (Prince *et al.* 1998). However, for the most part these trawl gear types are not distinguishable in the database. More recently, midwater or 'Gloria nets' have also been used, mainly in the winter fishery for blue grenadier (*Macruronus novaezealandiae*) off western Tasmania. The trawl fishery conducts some 25–35 thousand shots per year across the entire SEF. Shot-by-shot logbook data are available after 1985; however, the resolution and quality of these data vary substantially over time (Garvey 1998).

A base data set for further analysis was derived by subjecting the SEF1 database to a series of data quality tests. Both start and finish positions of the operation were required for high resolution analysis. Substantial numbers of operations had no finish position, or identical start and finish positions, and were excluded from the high resolution analysis. Also, spurious trawl tracks (derived from the start and finish positions) of over 30 nmile in length and those misreported as traversing land were excluded. Over the period 1995–99, data were of sufficient quality to treat each shot as a track with a start and finish position, although data screening still removed some 30% of operations for these years. For the 1986–99 period, spatial analyses were conducted at a low resolution (22 km), using the trawl start point and bottom-time hours as the unit of effort. High resolution data (1 km) using trawl tracks were analysed for the period 1995–99. Figure 1 illustrates the spatial disparity between the two data sets.

Analysis

All data treatments, presentations and statistical summaries where conducted within the ARC/INFO and Arcview GIS packages.

Low resolution

Effort in bottom-time hours was summed for trawl operations with start positions within the cells of a 22 km grid across the extent of the fishery, for the years 1986–99 inclusive. Over 96% of the trawl shots for the entire period were included in this analysis (Table 1).

High resolution

Start and end positions of operations were connected to generate simple straight line tracks. A 1 km grid was overlaid on these tracks and distance trawled was summed within each 1 km^2 cell. In a similar way to effort, grids of total catch were produced by apportioning catch equally along the length of trawl tracks and summing within 1 km cells. The Lambert Conformal Conic projection was the standard used in all spatial analyses to align with previous work. However, this projection causes slight errors in area and density calculations, therefore Albers Equal Area projection was used to correct for area distortions.

Logbook data from Commonwealth fisheries are confidential and the Australian Fisheries Management Authority (AFMA) has an operating rule of only presenting data aggregated from five or more vessels to protect vessel anonymity and 'secret' fishing localities. This

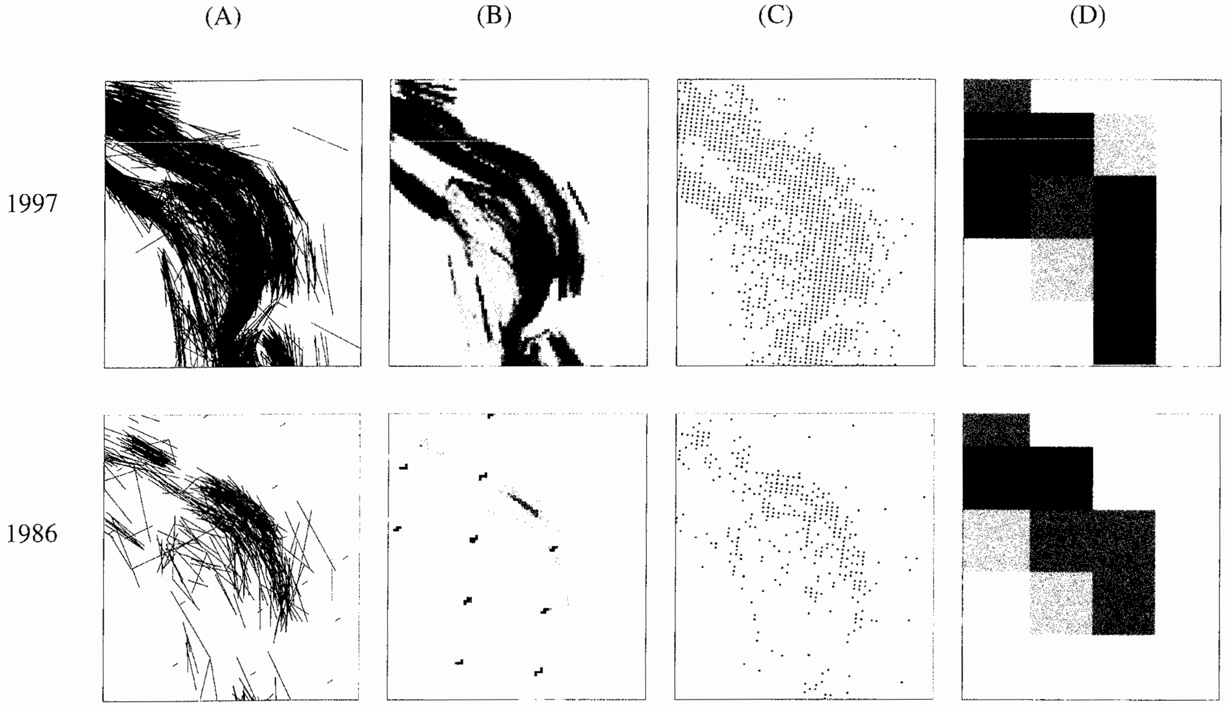


Fig. 1. Input data and output grids for 1986 and 1999. *(A)* Trawl tracks that were segmented and summarized (see Fig. 2) to produce *(B)* the 1 km grid of trawling effort (in length, analogous to swept area). *(C)* Shot start positions, each associated with an effort in hours. From this a second grid with a resolution of 22 km *(D)* was derived summing effort in hours from the start positions. In *A*, 1986 records containing only a start position were given an arbitrary length of 2 km to illustrate granularity of the data.

rule was applied to the map production, where cells with fewer than five boats represented are masked. Consequently, only an annual average of the years 1995–99 is presented in map form for the high resolution analysis, allowing a larger sample size and considerably less masking. This rule did not affect statistical summaries presented in table and graph form.

Table 1. Data preparation: percent of data remaining after successive data exclusion operations

Raw logbook data extracted by using a number of filters to produce a base data set. Base data were subjected to a series of more rigorous tests related to the availability of position information and the plausibility of the data. For each trawl shot these were availability of a start position, availability of both a start and end position, and a track <50 km in length. Base data set from the SEF1 logbook database, Australian Fishing Zone Information System: METHOD, otter trawl; ACTIVITY, 'fishing' or 'unrepresentative fishing'; excluding VESSELS Danish seine mis-labelled as otter trawl; EFFORT <10 h

Year	Base data set	Start position?	Start <> End position?	<50 km in length?
1986	100.0	99.9	99.8	97.6
1987	100.0	98.9	98.9	96.5
1988	100.0	97.3	97.3	95.4
1989	100.0	94.2	91.0	88.9
1990	100.0	93.1	85.8	82.8
1991	100.0	94.5	66.0	64.3
1992	100.0	95.6	59.1	56.9
1993	100.0	94.1	65.0	63.3
1994	100.0	97.0	73.2	71.4
1995	100.0	98.9	92.4	91.1
1996	100.0	98.6	93.1	91.5
1997	100.0	98.8	93.9	92.6
1998	100.0	98.7	91.6	90.1
1999	100.0	97.5	91.4	89.9
Overall	**100.0**	**97.1**	**86.3**	**84.4**

Results

Data quality

The data selection criteria resulted in poor data retention during 1990–94 (Table 1). This pronounced decrease in useable positional data was associated with three main factors: a gradual decline in the field support afforded by logbook maintenance officers until the early 1990s; the introduction of ITQ management that resulted in the logbook being used for quota monitoring purposes (under-reporting was particularly pronounced in 1992); and the existence of a jurisdictional loophole that allowed fishers to claim that catches made in Commonwealth waters had come from State waters and should therefore not be debited against their quota. The latter factor was resolved in 1994, but not before considerable misreporting of catch positions had occurred, particularly off New South Wales. In addition to this, before the widespread adoption of the Global Positioning System (GPS) for navigation, many earlier position data were reported on a grid system, and were consequently quite coarse in resolution (Fig. 1).

Coarse-scale temporal patterns in effort

Annual totals of trawl effort for the entire fishery (Fig. 2) declined slightly during 1986–92 (the 1992 total is most likely under reported), then rose markedly thereafter to a peak in 1997 of 101 000 h covering some 870 000 km of trawl track.

Total annual effort in hours trawled by statistical zone (Fig. 3*a*) and on a coarse-scale grid (Fig. 4) illustrates the shifts in the distribution of effort over 1986–98. In the mid 1980s, much of the SEF trawl effort was concentrated along the New South Wales coast and off Portland, Victoria. Then

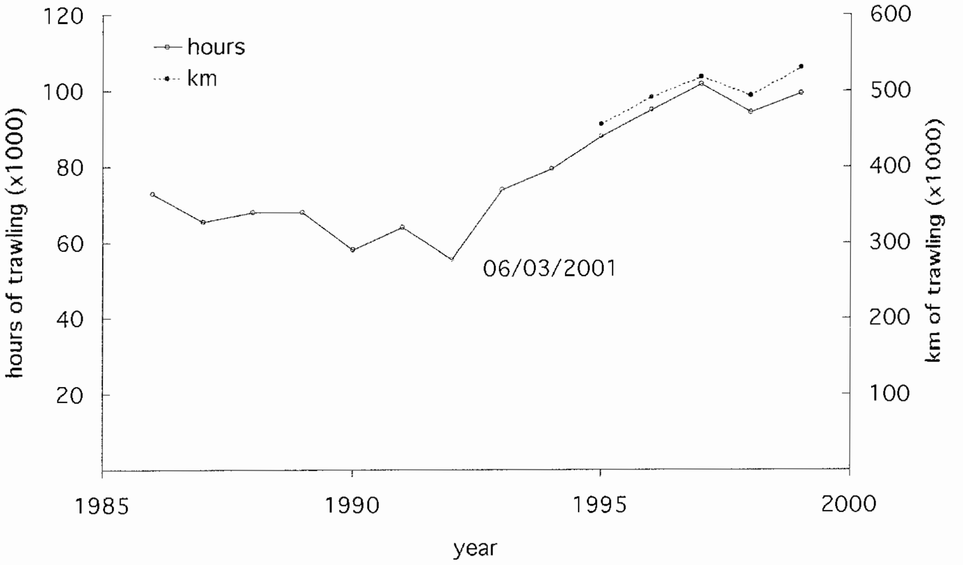


Fig. 2. Total effort in hours (1986–99) and corrected trawled distance (1995–99) for the SEF trawl sector. Retained data only (see Table 1).

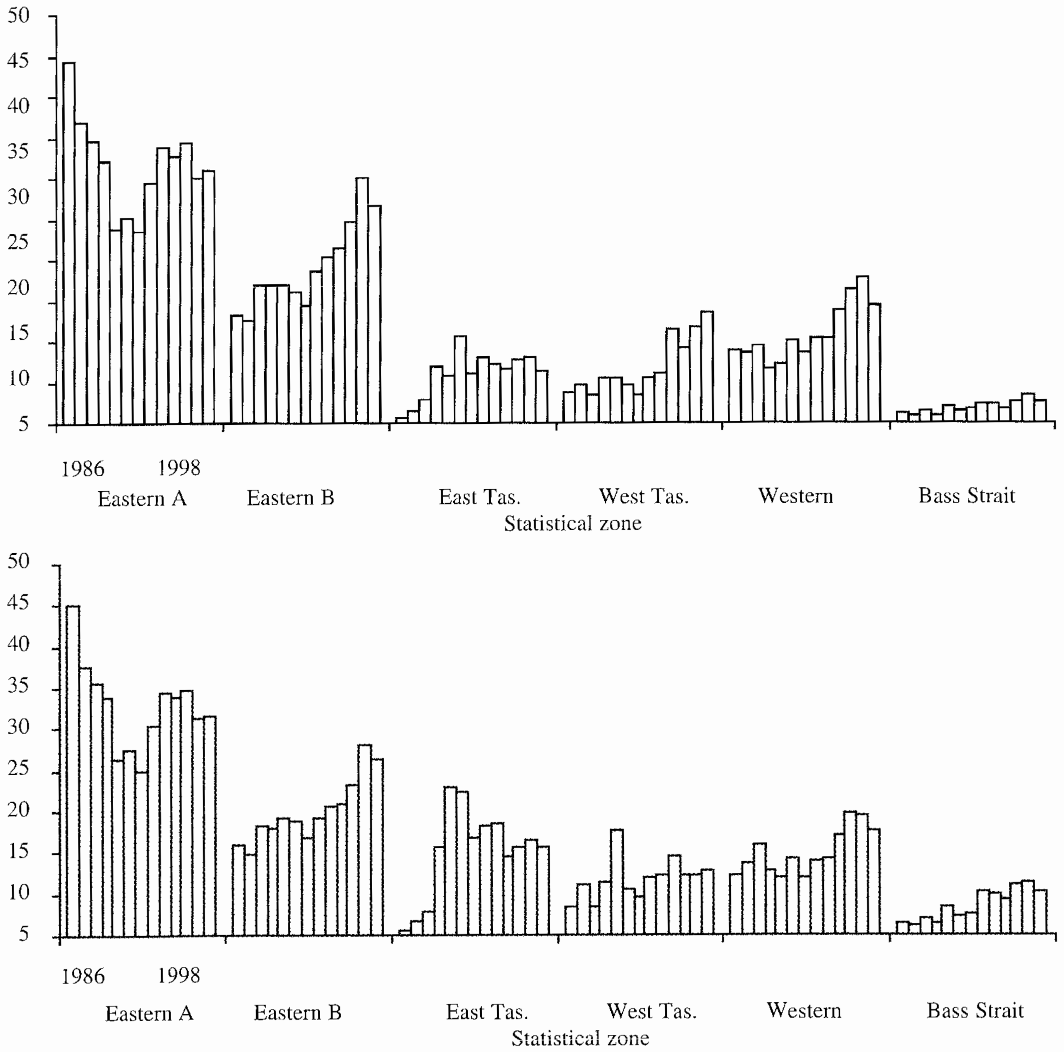


Fig. 3. SEF trawl effort in *(a)* hours and *(b)* number of shots, for 1986–98 by statistical area.

the discovery of major orange roughy (*Hoplostethus atlanticus*) fisheries off Tasmania during 1989–90 saw a transfer of effort to these waters (Tilzey 1994; Fig. 4). Because of the highly targeted nature of fishing orange roughy aggregations, with shots typically having a bottom-time of only a few minutes, hours trawled is a poor indicator of effort directed at this fishery. Thus, Fig. 3*a* does not adequately reflect the effort in the Eastern and Western Tasmania zones during this period. Figure 3*b* illustrates the marked increase in annual number of shots in these two zones during 1989–90. The subsequent decline of these orange roughy fisheries saw effort being diverted back into 'market' fishing, particularly in the Western zone and Eastern Sector B. From 1995 onwards, the development of the winter spawning fishery for blue grenadier off western Tasmania has also increased effort in this zone (Figs 3 and 4).

Fine-scale patterns in effort

On a finer scale it can be seen that the large trawl grounds of the SEF are reasonably well defined in terms of proximity to the edge of the continental shelf and sections of rough and untrawlable ground along the coast (Plate I). Inshore trawl grounds occur along the NSW coast, off Gabo Island and off Lakes Entrance, Victoria (not depicted in Plate I because of confidentiality requirements). The broadest area of high intensity trawl effort runs south of Eden (NSW) into the area known as 'The Big Horseshoe' in north-eastern Bass Strait. Other areas of intense effort occur along the NSW coast, off western Tasmania north of Strahan (the winter blue grenadier fishery) and along the coast from Portland, Victoria, to Beachport, South Australia. Heavily trawled orange roughy grounds, such as the St Helens and Maatsuyker seamounts, tend to be very small in area and are seen in Plate I as little more than points to the east and south

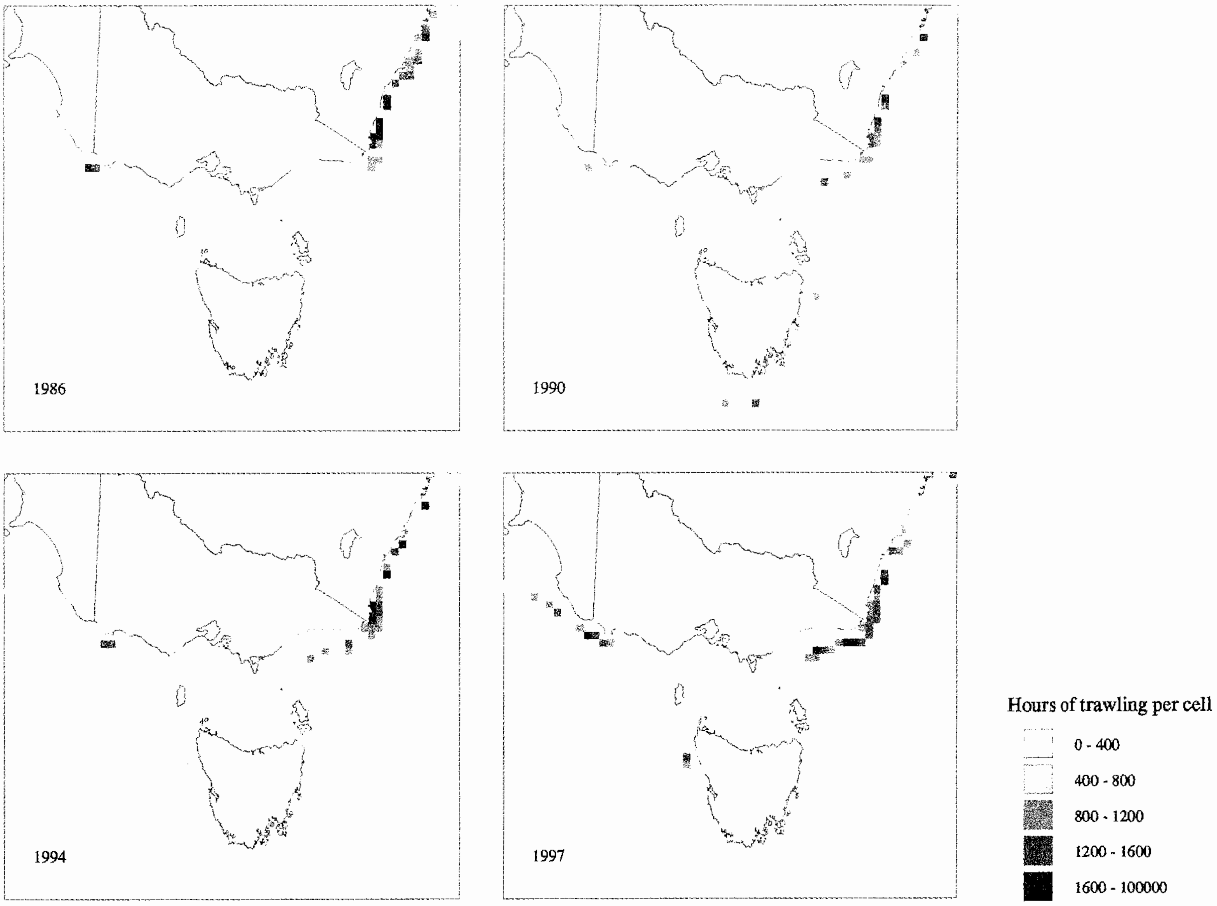


Fig. 4. Annual hours trawled per 22 km^2 cell for the years 1986, 1990, 1994 and 1997. Cells with <5 vessels represented are excluded to protect confidentiality.

of Tasmania. The extensive continental shelf shallows within the Bass Strait, Western Tasmania and Western zones are subject to little trawling. However, the SEF Danish seine fleet operates in north-east Bass Strait shelf waters.

Swept area

The amount of ground covered by the trawl gear, or swept area, may be defined variously, usually depending on the nature of the targeted species and its behaviour in relation to the trawl gear (Wardle 1997). Typical demersal trawl gear in the SEF comprises the trawl net itself, with a headrope length of 40–55 m, and sweeps of some 180–280 m in length, leading to the otter boards (Graham and Liggins 1995). In the absence of individual vessel gear data from the fishery, an 'average' trawl gear was defined for the purposes of swept area estimation (Fig. 5). Sweep width can be conservatively estimated from the headrope length at approximately 23 m (half the headrope length), or from the otter boards at approximately 140 m (assuming 230 m sweeps and a departure angle of 15°, see Fig. 5). Which of these interpretations is used is particularly significant in the context of assessing the intensity and extent of impact of trawl operations on benthic communities and ecosystems. The two sweep width estimates can be used as a guide for transforming the values reported below for distance trawled, into estimates of swept area.

Fine-scale statistics

The entire SEF as a management unit extends out to the EEZ boundary and covers some 1.17 million km^2. However, little fishing takes place outside the 1000 m isobath, and waters shallower than this comprise 255 thousand km^2. Some 42–45 thousand 1 km^2 grid cells were fished, representing 3.7% of total area (Table 2). After correcting for the data exclusion percentages in Table 1, the averaged annual distance trawled during 1995–99 was 537 435 km. This gives average annual swept area estimates of 12 361 km^2 and 75 240 km^2, based on the two values given above for gear width (although obviously much of this would involve trawling the same ground on more than one occasion).

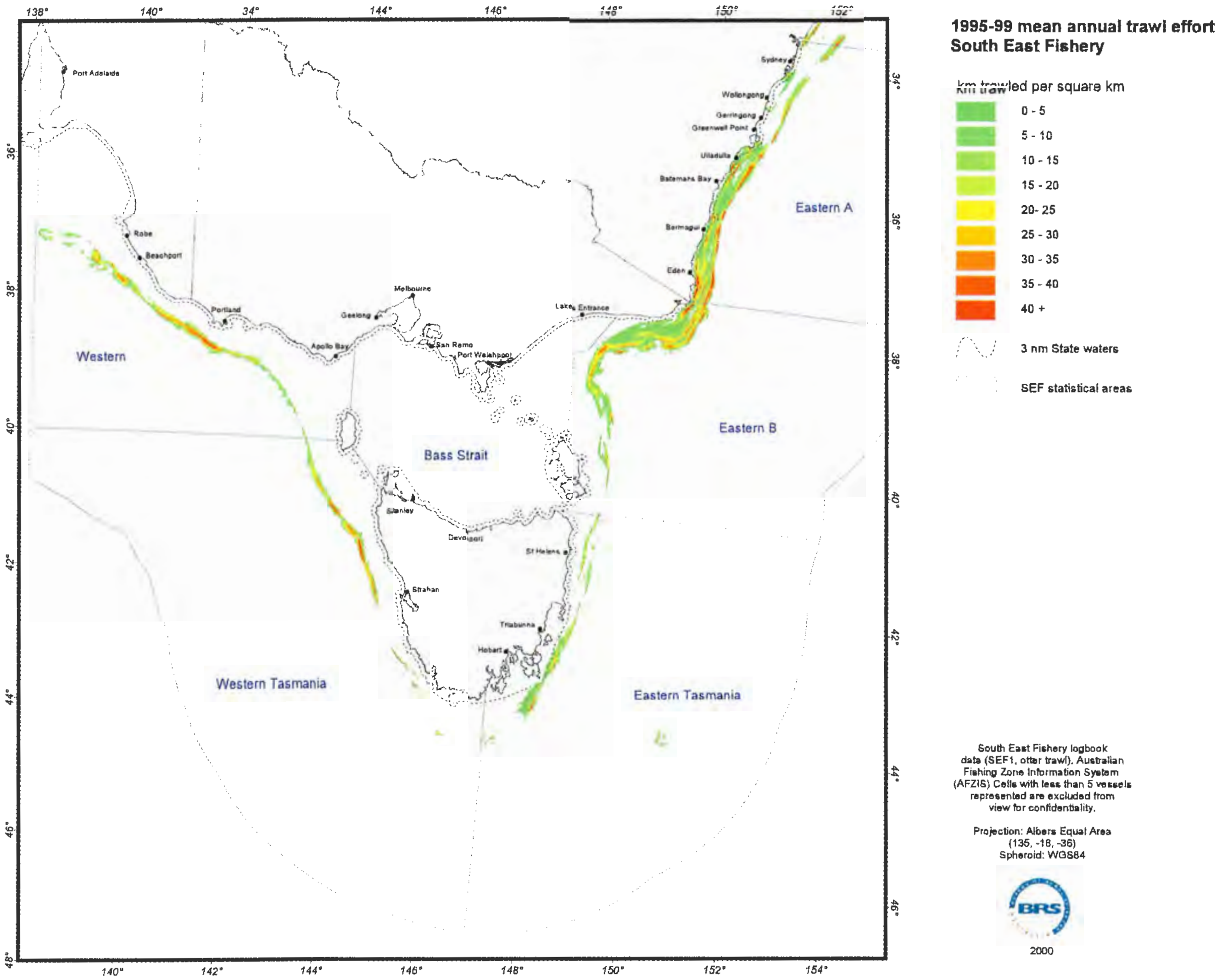


Plate I. Mean annual distance trawled per square kilometre, 1995–99. Statistical areas and Territorial Sea (3 nmile) baseline also shown. South East Fishery logbook data, Australian Fishing Zone Information System. Cells with <5 vessels represented are excluded from the analysis to protect confidentiality.

Figure 6 illustrates the extent of fishing in terms of the number of 1 km^2 cells fished, total effort and total catch within 5 km effort class intervals. Most of the fished cells are fished relatively lightly (Fig. 6*A*), with >50% of the cells falling into the lowest (0–5 km) effort class in all five years. The cells occupied by successive higher effort classes fall away until the aggregated 35+ km class. Conversely, a large proportion of the actual trawl effort (Fig. 6*B*) and catch (Fig. 6*C*) takes place in the comparatively small area of the 35+ km class.

Although the total area subject to fishing changed little over the years 1995–99 (Table 2, 1995–99 totals), there was substantial variability in the actual grids fished from year to year, with 56–61% of cells shared in annual comparisons between those fished and unfished (Table 3). This interannual variability tended to occur at the fringes of the main fishing grounds and almost exclusively comprised very low-effort cells. Interpreting these figures is difficult and must be undertaken with caution as a significant proportion of the apparent variability may arise from erroneous position data. A small number of trawls outside of the main ground, whether from genuine exploratory trawling or position errors, has a large influence on estimates of both the total cells fished and the proportion of shared cells.

The period 1995–99 saw an overall increase in the area subject to high intensity (35+ km) fishing, peaking in 1997 at 6.9% of the total area subject to fishing (Fig. 6*A*). Similarly, the percentage of total effort (km) occurring within the high intensity cells increased from 28.6% to 34.47% between 1995 and 1997 (Fig. 6*B*). This result suggests that a redistribution or increase in effort tended to further concentrate in high intensity areas, rather than increasing across the overall fished area or spreading to new areas, over this period.

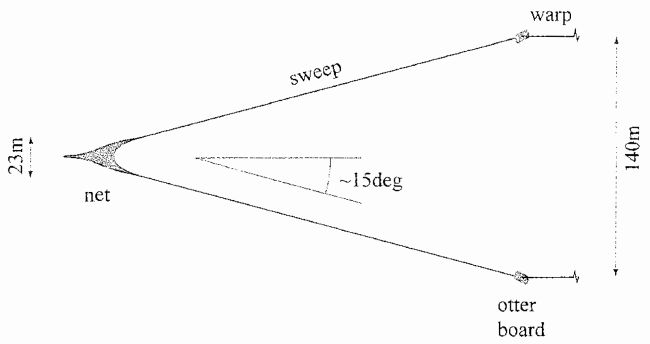


Fig. 5. Typical SEF otter trawl gear indicating swept area at the headrope (net) and of the entire gear from the otter boards.

Statistical zones

Because little fishing takes place at depths >1000 m, statistical zones were redefined as depths <1000 m to provided a more useful summary of effort distribution (Table 2, see Plate I for statistical areas). Overall, out of 255 279 1-km^2 cells in waters <1000 m depth, an average of 34 627 or 13.5% of cells were fished for the years 1995–99. This proportion varied from less than 10% in the Eastern and Western Tasmania zones, to 70% in Eastern Sector B (Fig. 7*A*). A similar pattern was seen for annual effort (km) within each statistical zone (Fig. 7*B*). The highest effort of almost 200 000 km of trawling was estimated for Eastern Sector A, followed by Eastern Sector B and the Western zone, with the two Tasmanian zones each subject to approximately 50 000 km of trawling. As recorded in Plate I, increases in effort over 1995–99 were evident in Eastern Sector B and the Western zone. Catches by statistical area showed a similar pattern (Fig. 7*C*) with the exception of Western Tasmania where catches and catch rates of blue grenadier (*Macruronus novaezealandiae*) from a winter spawning aggregation fishery were high.

Depth strata

As mentioned previously, only a minor proportion of the SEF continental shelf is subject to trawling, with ~10% of the cells in the 0–200 m depth range being fished (Fig. 8*A*). It should be noted that these waters are also trawled by state licensed vessels, outside the scope of the study. Shelf-break and slope grounds between 200 and 1000 m depth are fished more extensively, with over one half the grids being fished (Fig. 8*A*). Because of the far greater area of the shelf compared with these slope grounds (Table 4), the actual amount of effort (km) directed at the shelf is similar to that for slope grounds (Fig. 8*B*). However, a significantly greater proportion of the catch comes from the upper continental slope, in waters deeper than 200 m (Fig. 8*C*). Over 1995–99 there was a slight increase in the percentage of slope cells fished (Fig. 8*A*) and an increase in effort and catch on grounds inside the 600 m isobath (Figs 8*B*, 8*C*).

Discussion

Background

The shifts in fishing effort described here should be viewed in the context of what was happening in the management of the fishery. The period monitored by the logbook has encompassed some sweeping changes in SEF management practice and fleet behaviour. Before 1985, there were few restrictions placed on fleet capacity (Tilzey 1994). Boundaries and limited entry management were first introduced in 1985, together with a boat replacement policy that was linked to a boat-unitization system in 1986. The central aim of this management plan was to gradually reduce fleet capacity and an important component of the boat replacement policy was the forfeiture to the Commonwealth of a specified proportion of units of capacity when upgrading or replacing a vessel. In the late 1980s, the downturn in the eastern stock of gemfish (*Rexea solandri*), then the largest volume component of the SEF, accompanied the development of the orange roughy fishery. The upsurge in demand for the units needed to obtain vessels large enough to participate in the latter fishery caused about 10 east coast based operators to sell out of the SEF. There was consequently a shift in effort from the Eastern Sector zones to waters off Tasmania during this period. The input management controls failed to stop additional vessels entering the fishery via successful legal appeals. By the time output management controls in the form of TACs and ITQs were introduced at the start of 1992,

Table 2. Number of 1 km^2 cells above 1000 m depth subject to fishing in each statistical zone, 1995–99

Also given: total area and total above 1000 m area of each statistical area. See Plate I for statistical zones

Zone	Zone area	0–1000 m area	No. fished cells				
			1995	1996	1997	1998	1999
Eastern A	246971	17674	12974	13095	12711	12302	12586
Eastern B	169482	28571	12426	11876	11600	12082	12958
Eastern Tas.	274470	21105	5303	5733	5824	5083	4699
Western Tas.	335209	30306	5179	4902	4877	4854	5626
Western	146091	62439	5723	6857	7262	6768	7190
Bass Strait	96715	95184	1050	1004	1603	1720	1914
Totals	1172223	255279	42655	43467	43877	42809	44973

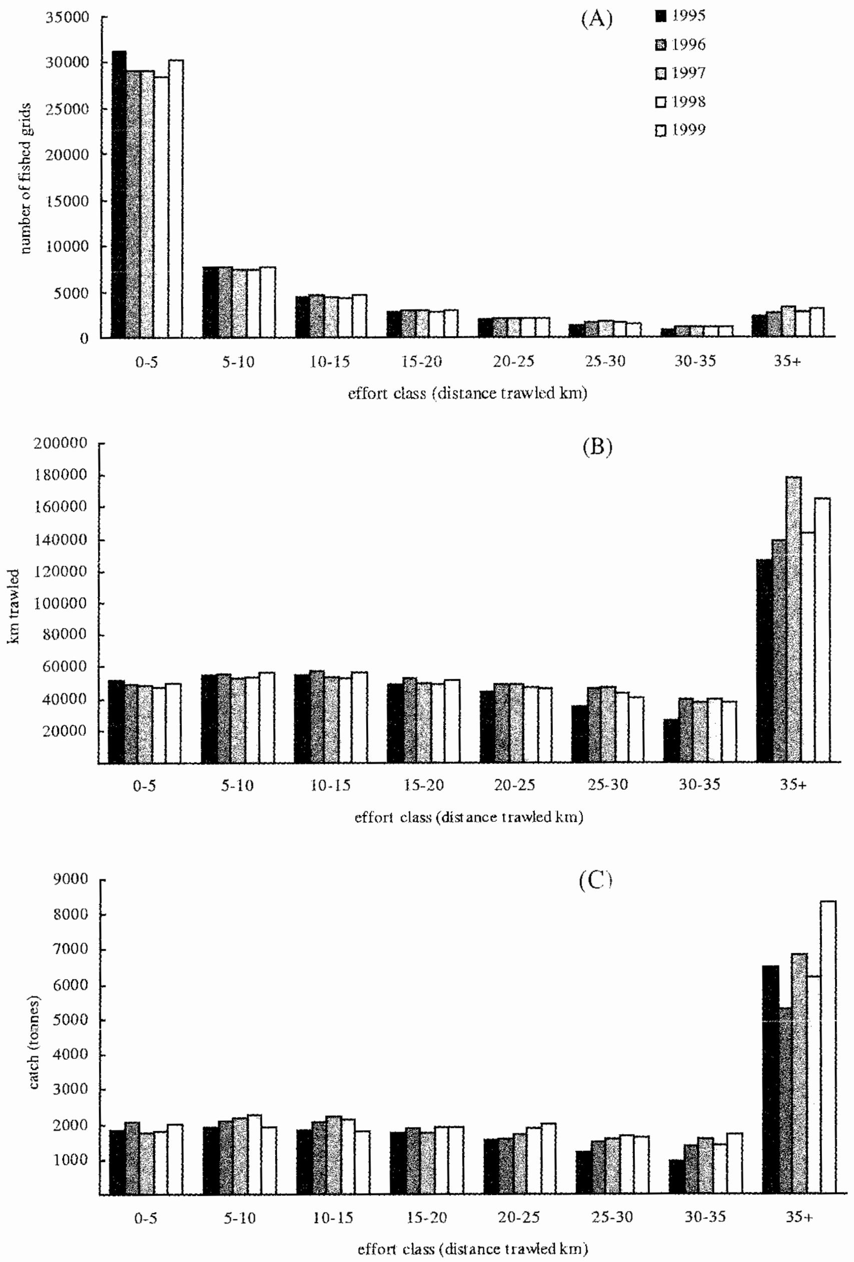


Fig. 6. 1995–99: *(A)* frequency breakdown of grid cells by effort classes; *(B)* frequency breakdown of distance trawled by effort classes (km); and *(C)* frequency breakdown of total catch by effort classes.

the number of units of capacity in the fishery had increased from 24 086 in 1986 to 24 664, rather than declining (Tilzey 1994). Hence, although there was a significant fall in effort in Eastern Sector A from 1986 to 1990, overall SEF effort did not alter appreciably during this period.

Effort distribution and intensity

Trawl effort in the SEF, as measured in hours and distance trawled, has steadily risen since the introduction of ITQ management, but showed a 7% downturn (hours) from 1997 to 1999. In real terms, fishing effort has probably risen more sharply as the fleet's fishing power has increased. For the period 1995–97, when high spatial resolution analysis was possible, it was evident that this increase did not involve development and expansion to new grounds but rather intensification within existing grounds. Further, the additional effort appears to be concentrating in relatively small, high effort areas, rather than increasing equally across the grounds. In 1997, 4354 (9%) of the total fished km^2 cells, received 35 km of trawling or more (Fig. 6*A*). On

Table 3. Overlap comparison of fished and unfished cells for the years 1995–99

Shared cells were fished in both years, non-shared cells were fished in one year but not the other. Values are percentages of the total fished cells from both years shared

non-shared	1 km cells	1995	1996	1997	1998	1999
	1995	100	58	56	56	56
	1996	42	100	61	59	58
	1997	44	39	100	61	59
	1998	44	41	39	100	61
	1999	44	42	41	39	100

the basis of the gear dimensions illustrated in Fig. 5, these cells were potentially fully swept close to once or more by the trawl net itself and five or more times by the entire gear (including sweeps). Similarly, 666 km^2 (1.4%) received 80+ km of trawling and 148 km^2 (0.3%) received 120+ km of trawling.

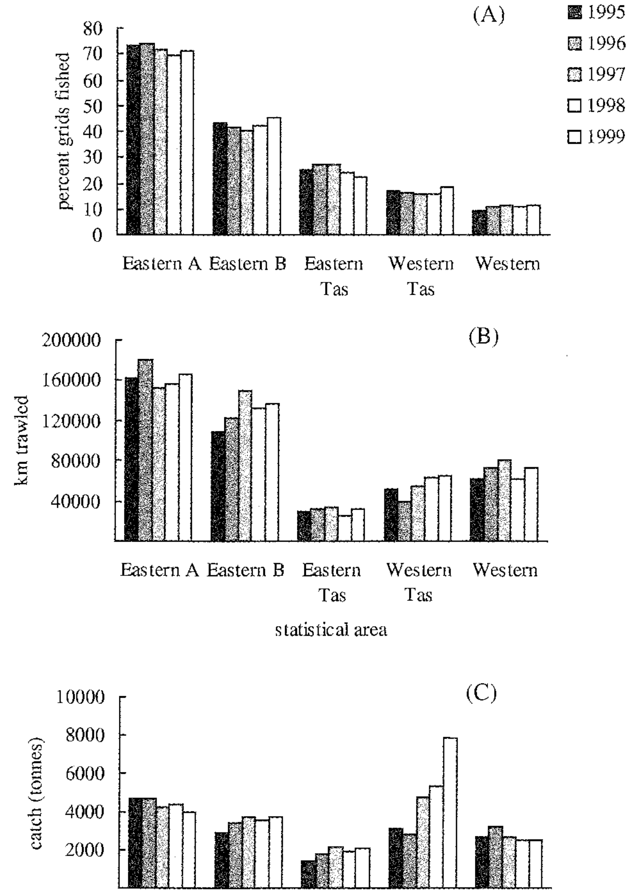


Fig. 7. *(A)* Proportion of grid cells fished in the 0–1000 m depth range within each statistical area; *(B)* distance trawled within the 0–1000 m depth range of each statistical area; and *(C)* total catch within the 0–1000 m depth range of each statistical area 1995–99. Note data selection criteria (Table 1).

All fishery logbook data are limited in spatial precision. In the North Atlantic, most fisheries data are reported by large statistical areas, covering over 4000 km^2 in some cases (Meaden and Kemp 1996). Conversely, in the SEF trawl and in an increasing number of other fisheries, operations data may be reported at the limit of GPS navigation precision (30–100 m). In practice, SEF data were limited by the precision at which the original position was recorded in the log and the decimal precision of the location field in the database. The fine scale 1 km resolution used in the present work was the result of this latter limitation. Forty kilometres of trawling in a grid square could, at one extreme, represent one swathe swept 40 times or, at the other extreme, the whole square swept once by the trawl net only, or 5.6 times by the full sweep of the gear described in Fig. 5.

In an analysis of micro-scale beam trawl effort in the North Sea, Rijnsdorp *et al.* (1998) found that operations were randomly distributed below a spatial scale of 1 × 1

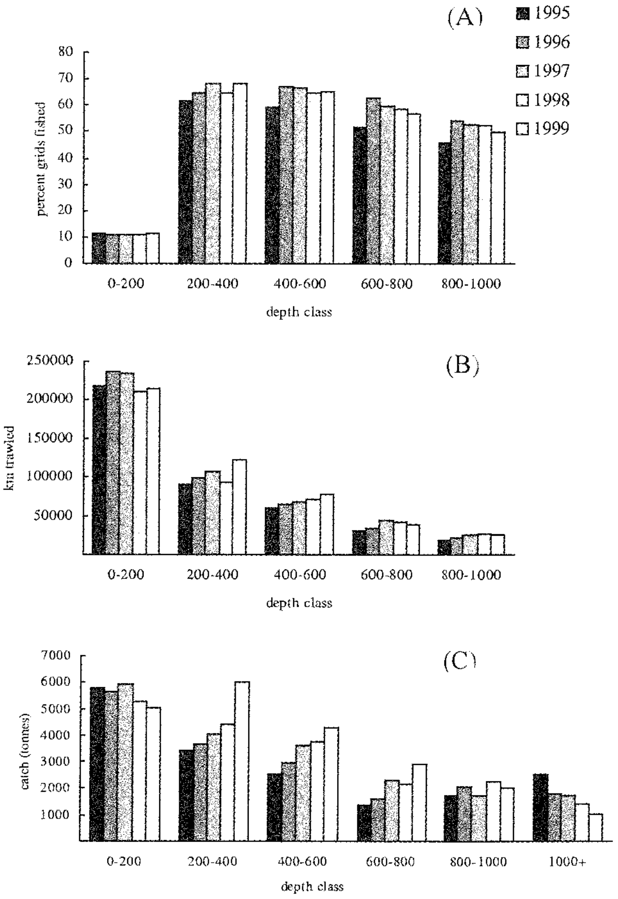


Fig. 8. *(A)* Percentage of grid cells fished within each depth stratum; *(B)* distance trawled within each depth stratum; and *(C)* total catch within each depth stratum 1995–99.

Table 4. Total depth stratum areas and number of 1 km^2 grid cells subject to fishing within each depth stratum, 1995–99

Depth (m)	Stratum area (km)	1995	1996	1997	1998	1999
0–200	327648	11.3	10.7	10.9	10.7	11.6
200–400	14926	61.9	64.7	68.2	64.4	67.8
400–600	11338	59.2	67.1	66.5	64.4	65.1
600–800	9006	51.5	62.8	59.6	58.5	56.8
800–1000	9318	46.0	54.0	52.9	52.4	49.6

nmile (1.85 × 1.85 km) and patchily distributed at scales greater than this. In the Australian Northern Prawn Fishery, Stobutzki and Pitcher (1999) found effort to be highly aggregated at a very fine scale within a 6 nmile grid, and that large areas within high effort grids may remain lightly trawled or untrawled. Interviews with trawl fishers in the SEF indicate that the precision of net placement in the SEF may be quite high (<1 km), even at the considerable depths (>800 m) in which the gear is often deployed. Prince *et al.* (1998) noted that fishers were placing their trawl gear more accurately and closer to reefs and rough grounds with the aid of GPS plotters and acoustic equipment. Trawling is routinely undertaken in relatively narrow depth strata on the upper continental slope (200–1000 m depth) to target particular suites of species. Because gradients on the upper slope are often steep, gear must be positioned very accurately (<1 km) to stay within a 100 m depth range.

It is probable that there is considerable spatial structuring of trawl effort below a scale of 1 km and that small areas may be swept in a structured, non-random manner. Acquiring a volume of detailed trawl track data from GPS plotters used in the various SEF statistical zones would be extremely useful for addressing some of these questions. Satellite vessel monitoring systems (VMS) also have the potential to provide highly precise positions of the vessel, if not directly of the gear itself. There also appears to be potential to use statistical techniques such as maximum entropy tomography (Vignaux *et al.*1998) to better quantify effort and catch distribution with current logbook data.

One of the aims of this work was to better define the areas trawled within the SEF trawl and to detect changes in the fishing grounds since 1986 when detailed (trawl-by-trawl) logbooks were introduced. The data were unable to support this objective satisfactorily for the period 1986–94 and the study was partly confined to the period 1995–99 when the resolution and coverage of the data were considered adequate. A first look at the raw statistics of overlapping cells (Table 3) indicated large interannual changes in the trawled areas, but these should be interpreted with caution given the methodology used. In general, the changes occurred at the fringes of high intensity areas, comprised low-effort cells and represented a very small proportion of the total effort. Some of this effort was undoubtedly from erroneous position reporting, but the extent of misreporting was impossible to determine with the present data. When defining a 'trawl ground' at some scale it is necessary to define a minimum amount of effort for inclusion of a cell in area calculations and for subsequent comparisons between periods. Selection of this minimum would be a somewhat subjective exercise but could be based on potential proportion of the cell swept.

Despite the spatial shift in effort and the opening up of new deepwater grounds that have occurred since 1986, the fine scale analysis for 1995–99 indicates that fishers are largely adhering to established grounds. The only new trawl grounds to have been established since 1995 are the 'offshore' deepwater fisheries on the Cascade Plateau and the South Tasman Rise. The increasing concentration of effort into high intensity areas is most likely caused by several factors. Limited trawl ground availability is a major factor off Portland, Victoria, where a comparatively narrow strip of trawlable ground is abutted by large areas of untrawlable reef. The localized nature of high-volume spawning fisheries such as the winter blue grenadier fishery off western Tasmania and the orange roughy fishery on St Helens 'Hill' off eastern Tasmania is another major factor. Finally, with the use of GPS plotters, operators are now able to accurately repeat trawl tracks in selected areas.

Marine disturbance

Some general comments may be made on the interpretation of the present results in terms of quantifying and interpreting potential marine disturbance. Biological and physical effects of trawling have been discussed and reviewed (e.g. Jones 1992; de Groot *et al.*1994; Hall 1994; Auster *et al.*1996; Poiner *et al.*1998), with most attention focussed on perturbation of the substrate by the gear (furrowing and flattening), resuspension of sediments and direct and indirect mortality of organisms. There have been no published studies of the effect of trawl gear on benthic communities as a whole on the outer continental shelf and upper slope in southern Australia. From replicated trawl surveys in Eastern Sector A, Andrew *et al.*(1997) found marked changes in the comparative abundance of upper continental slope fishes between 1976–77 and 1996–97, including a 62% decline in commercial fish species, and strongly inferred that sustained fishing (predominantly trawling) over this period was the major cause. As with many other fisheries world-wide, there is now limited potential for undertaking a Before After Controlled Impact type experiment to quantify trawl effect. In the case of the Andrew *et al.* (1997) surveys, it should be noted that when the initial surveys were carried out in 1976–77, little commercial trawling had previously been carried out in the upper slope areas surveyed.

The effect of trawling and repeat trawling (over the same ground) is to some extent dependent on the component of the biota that is being measured. Sainsbury *et al.* (1992) found up to 90% removal of large sponges after a single trawl on the North West Shelf of Australia. Poiner *et al.*(1998) estimated a 5–25% removal of benthos by a single pass of a prawn trawl in Northern Great Barrier Reef waters, with multiple passes having a cumulative effect such that seven trawls removed about half the benthos. The implications of this effect, in terms of the rate of recovery of the benthos and community structure, were unclear. Trawlers in the SEF use both lightweight gear with chain ground ropes (particularly in the northern part of the Eastern A zone) and heavy trawl gear with rubber discs and bobbins to contend with rough ground (Graham and Liggins 1995). This heavy gear has been found to have a greater effect on the benthos than lightweight prawn trawl gear (Gordon *et al.*1998). At present, only broad spatial usage patterns of these various gears are known for SEF trawlers. In the major trawl grounds, on and adjacent to the upper continental slope, it seems likely that some parts of the seafloor are swept in excess of 10 times per year.

In recent years (1995–99), the vast majority of trawl operations have occurred within established fishing grounds. It is likely that new grounds are still being developed, but at fine scale, particularly at the fringes of established grounds adjacent to and amidst reefs and rough ground (Prince *et al.* 1998). The spatial resolution of the current work is insufficient to detect these changes, particularly over such a short time period.

Analysis of catch rates

Catch rates obtained from logbooks are the primary source of relative fish abundance information in the SEF, and one of the key uncertainties in recent stock assessments (Tilzey 1999). A considerable amount of analysis has been directed towards accounting for factors such as season, vessel, lunar phase, depth, time and latitude to improve the accuracy of catch rates as an index of abundance. Generalized linear or additive modelling are the favoured statistical tools to remove the effect of these factors. Standardizations have not, to date, accounted for changes in fishing behaviour, particularly as a response to management arrangements such as the introduction of the quota system in 1992. Interpretation of the spatial nature of the SEF has been relatively crude, relying on simple latitude area blocks or statistical zones. The quite well defined trawl grounds, evident in this study, should provide a useful starting point for a more integrated approach that accounts for the spatial structuring of the fishery itself, rather than convenience factors such as latitude. A preliminary appraisal of the 1995–99 fine-scale effort (Plate I) along with bathymetric and catch composition data suggests that there are of the order of 100 identifiable trawl grounds that are regularly fished in the SEF. With further development, including input from fishers, a representative classification of trawl grounds should prove useful for catch rate standardization and the planning and implementation of trawl surveys for assessment purposes.

Acknowledgments

We thank Ken Graham (NSW Fisheries Research Institute) for advice regarding trawl gear, and the Australian Geological Survey Organisation for the provision of bathymetry. We are also grateful to the trawl fishers of the SEF for continuing to provide valuable logbook information. This work was supported by the Fisheries Resources Research Fund.

References

Andrew, N. L., Graham, K. J., Hodgson, K. E., and Gordon, G. N. G. (1997). Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. NSW Fisheries Final Report Series, Dec 1997, No. 1. 200 pp. (NSW Fisheries: Cronulla, Australia.)

Auster, P. J., Malatesta, R. J., Langton, R. W., Watling, L., Valentine, P. C., Donaldson, C. L. S., Langton, E. W., Shepard, A. N., and Babb, I. G. (1996). The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (northwest Atlantic): implications for conservation of fish populations. *Reviews in Fisheries Science* **4**(2), 185–202.

De Groot, S. J. (1984). The impact of bottom trawling on benthic fauna of the North Sea. *Ocean Management* **9**, 177–90.

Garvey, J. (1998). Resource information for fisheries management. Pilot study: an evaluation of the South East Fishery logbook program. Final report to the Fisheries Resources Research Fund (FRRF), Bureau of Resource Sciences, Canberra, 35 pp.

Gordon, D. C., Schwinghamer, P., Rowell, T. W., Prena, J., Gilkinson, K., Vass, W. P., and McKeown, D. L. (1998). Studies in eastern Canada on the impact of mobile fishing gear on benthic habitat and communties. Effects of Fishing Gear on the Sea Floor of New England, Conservation Law Foundation 1998, 63–67.

Graham, K. J., and Liggins, G. W. (1995). NSW continental shelf trawl-fish survey: gear, gear trials and preliminary sampling. NSW. Fisheries Kapala Cruise Report No. 113. 14 pp. (NSW Fisheries: Cronulla, Australia.),

Greenstreet, S. P. R., Spence, F. B., Shanks, A. M., and McMillan, J. A. (1999). Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. II. Trends in fishing effort in the North Sea by UK registered vessels landing in Scotland. *Fisheries Research* **40**, 107–24.

Greenstreet, S. P. R., and Hall, S. J. (1996). Fishing and the groundfish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology* **65**, 577–98.

Grieve, C., and Richardson, G. (2001). Recent history of Australia's South East Fishery; a manager's perspective. *Marine and Freshwater Research* **52**, 377–86.

Hall, S. J. (1994). Physical disturbance and marine benthic communities: life in unconsolidated sediments. In 'Oceanography and Marine Biology: an Annual Review (Vol. 32)'. (Eds A. D. Ansell, R. N. Gibson and M. Barnes.) pp. 179–239. (UCL Press: London.)

IMCRA Technical Group (1998). Interim Marine and Coastal Regionalisation for Australia: an ecosystem-based classification for marine and coastal environments. Version 3. 3. (Environment Australia, Commonwealth Department of the Environment: Canberra.) 102 pp.

Jones, J. B. (1992). Environmental impact of trawling on the seabed: a review. *New Zealand Journal of Marine and Freshwater Research* **26**, 59–67.

Klaer, N. L., and Tilzey, R. D. J. (1994) The multi-species structure of the South East Fishery. In 'The South East Fishery'. (Ed. R. D. J. Tilzey.) pp. 72–94. (Bureau of Resource Sciences, Australian Government Publishers: Canberra.)

Meaden, G. J., and Kemp, Z. (1996). Monitoring fisheries effort and catch using a geographical information system and a global positioning system. In 'Developing and Sustaining World Fisheries Resources'. Proceedings of the World Fisheries Congress, Brisbane (Australia): the State of Science and Management, 28 July–2 August 1997. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. P. Beumer.) pp. 238–44. (CSIRO Publishing: Melbourne.)

Poiner, I., Glaister, J., Pitcher, R., Burridge, C., Wassenberg, T., Gribble, N., Hill, B., Blaber, S., Milton, D., Brewer, D., and Ellis, N. (1998). Final report on the effects of trawling in the far northern section of the Great Barrier Reef: 1991–1996. (CSIRO Division of Marine Research: Cleveland, Australia.)

Prince, J., Baelde, P., and Wright, G. (1998). Synthesis of industry information on fishing patterns, technological change and the influence of oceanographic effects on fish stocks in the South East Fishery. Final Report to Fisheries Research & Development Corporation, 97/114, 36 pp.

Rijnsdorp, A. D., Buys, A. M., Storbeck, F., and Visser, E. G. (1998). Micro-scale distribution of beam trawl effort in the North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES Journal of Marine Science* **55** N3, 403–19.

Sainsbury, K. J., Campbell, R. A., and Whitelaw, W. (1992). Effects of trawling on the marine habitat on the North West Shelf of Australia and implications for sustainable fisheries management. In 'Sustaining Fisheries through Sustaining Habitat'. (Ed. D. A. Hancock.) pp. 137–45. (Bureau of Resource Sciences. Australian Government Publishing: Canberra.)

Stobutzki, I., and Pitcher, R. (1999). Assessing the response of bycatch communities to prawn trawling. In 'Establishing Meaningful Targets for Bycatch Reduction in Australian Fisheries'. Australian Society for Fish Biology workshop proceedings, Hobart, September 1998. (Eds C. D. Buxton and S. E. Eayrs.) (Australian Society for Fish Biology: Sydney.)

Tilzey, R. D. J (Ed.) (1994). 'The South East Fishery.' (Bureau of Resource Sciences, Australian Government Publishers: Canberra.) 360 pp.

Tilzey, R. D. J. (Ed.) (1999). The South East Fishery 1998, Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Vignaux, M., Vignaux, G. A., Lizamore, S., and Gresham, D. (1998). Fine-scale mapping of fish distribution from commercial catch and effort data using maximum entropy tomography. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1220–7.

Ward T., Butler, E., and Hill, B. (1998). 'Environmental indicators for national state of the environment reporting – Estuaries and the Sea, Australia: State of the Environment (Environmental Indicator Reports).' (Department of the Environment: Canberra.)

Wardle, C. S. (1997). Investigating the behaviour of fish during capture. In 'Developments in Fisheries Research in Scotland'. (Eds R. S. Bailey and B. B. Parrish.) pp. 139–55. (Farnham Fishing News Books: Aberdeen.

Manuscript received 22 November 1999; revised and accepted 13 November 2000

Mar. Freshwater Res., 2001, **52**, 431–49

Ecosystem of the South East Fishery (Australia), and fisher lore

Jeremy D. Prince

Biospherics P/L, PO Box 168, South Fremantle, WA 6162, Australia

Abstract. A description of the marine ecosystem that sustains fisheries production around south-eastern Australia is based on a synthesis of fisher lore of the demersal trawling sector, a review of the literature and a decade of the author's field observations. A wide range of species are fished demersally in the South East Fishery (SEF). Until recently, managers and researchers have often implicitly assumed that many of these demersally caught species were neritic and lived in close association with the seabed. In contrast, fisher lore emphasizes the pelagic and oceanic nature of the commercial resource together with its environmentally forced variability. This paper substantially supports the views of the fishers. Up to 90% of the primary production of the SEF ecosystem may be garnered by fish foraging through extensive, but relatively sparse, oceanic phytoplankton and gelatinous zooplankton communities. Sporadically, climatic conditions cause oceanographic features to interact with shelf-break features and create ephemeral hotspots of primary production along the shelf break. Fish of the SEF take advantage of these productivity events to aggregate for feeding and breeding and their episodes of aggregation and dispersion cause the large seasonal variations in catchability observed with the shelf-break species. Implications for ecosystem management are briefly discussed.

Introduction

The primary purpose of this paper is to review knowledge about the marine ecosystems that sustain fisheries production in the South East Australian Fishery (SEF). Central to this aim is discussion of the extent to which the ecosystem is demersal and neritic (shelf bound), or a pelagic oceanic resource; this question has been the cause of considerable debate between biologists and fishers working in the SEF, and the answer determines the extent of the primary production available to sustain the SEF ecosystem, the importance of protecting benthic habitats, and the degree of robustness of SEF species to overfishing.

Of key interest to understanding the size, productivity and dynamics of SEF ecosystems is an understanding of the mechanisms by which the primary production is garnered, and the area over which it is collected. What is the catchment area for the primary production of the SEF? And what is the relative importance of primary production over the continental shelf and slope to the SEF? Is it the entire base of the SEF ecosystem, or a part of a larger area of primary productivity?

Knowledge of the SEF ecosystem has been generated principally through trawling and acoustics. However, the size of pelagic and demersal trawls, along with the speed of trawling, directly affects the catchability of fish and squid (Aron and Collard 1969; Clark 1973, 1978; Brooks *et al.* 1974; Gjøsaeter and Kawaguchi 1980; Pearcy *et al.* 1982; Gordon and Duncan 1985; Kenchington 1989; Koslow *et al.* 1997). Larger and more mobile species of fish and most squid effectively avoid being captured by trawls. Further, trawls smash the fragile gelatinous zooplankters that are a significant component of SEF ecosystems, so that they cannot be studied. Finally, the absence of swim bladders or hard body parts and the possession of certain body shapes make gelatinous zooplankton, squid and some fish invisible to acoustic studies (Koslow *et al.* 1997).

Studying the composition of the deep scattering layers associated in the SEF, Hall and Quill (1983) found no fish heavier than 3 g in their pelagic trawls despite the indication by acoustic profiles that a considerable amount of larger species was present. Similarly, Koslow *et al.* (1997) detected larger fish (200–1300 g) with gas-filled bladders throughout the water column excepting surface layers but could not catch them with mid-water trawls. Using acoustics and mid-water trawls, Williams and Koslow (1997) concluded that their mid-water trawls were sampling only 4–14% of the available biomass. Gjøsaeter and Kawaguchi (1980) noted that in the study of these deep-water and oceanic ecosystems all the sampling techniques are at best semi-quantitative. All have inherent biases, leaving considerable room for conjecture about the SEF ecosystem.

The basis of this study has been analysis of the lore related to me by the fishers of the SEF since I began working with them in 1992. There has been no attempt to 'randomize' my sample of SEF fishers, but I have spoken to almost every fisher in the fishery. Individuals widely recognized as exceptional fishers were especially consulted. Skilful fishers base their prowess on observations of marine

10.1071/MF00042 1323-1650/01/040431

systems (Johannes 1981, 1998), so of particular interest have been the observations on which the fishers base their opinions about the SEF ecosystem. Directed by my synthesis of fisher lore, I have reviewed the literature. Here, I concentrate on local rather than international research. Where possible, I have used the literature and my own field data to test the veracity of the fisher lore.

Fishing lore in the SEF

Fishing of feed layers

Fishers in the SEF believe they fish an ecosystem that extends out of the deep mid water of the adjacent oceans onto the continental slope and into shallower shelf waters. Such opinions are based on many hours of watching echosounders and studying the behaviour of the acoustically reflective deep scattering layers. The fishers call the deep scattering layers 'feed layers', believing they contain the prey of the commercial species. From their own catches the fishers know that the 'feed layers' do not always contain commercial species, but when over trawl grounds, the commercial species are expected to be associated with such layers.

Off New South Wales (NSW, Fig. 1), fishers describe a seasonal cycle in the densities of the feed layer that they believe is an annual succession of species within the mid-water ecosystem (Prince 1996). During autumn and winter each year, fishers watch the density of feed layers start to build up over their trawl grounds. Initially each winter, the feed layers contain only 'blubber' (gelatinous zooplankton), but as the season progresses there is an increasing amount of 'prawns' (actually a wide range of crustaceans) in their catches. Next, the fishers observe increased quantities of small fish, including lantern fish (Myctophidae) and whiptails (Macrouridae), followed by jack mackerel (*Trachurus declinus*) and eventually larger piscivorous fish such as southern frostfish (*Lepidopus caudatus*) and gemfish (*Rexea solandri*).

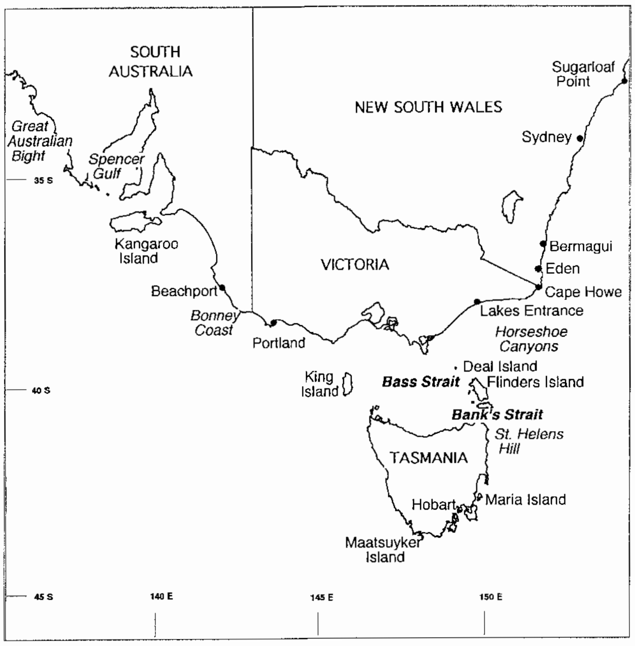


Fig. 1. Map of the area covered by the South East Fishery, Australia.

The typical feed layers observed by fishers descend at dawn (Plate I). Integration of the strength of acoustic returns from above 400 m in echograms such as in Plate I shows that total acoustic biomass in the water column declines daily around daybreak by ~90% (Prince *et al.* 1997). Fishers believe that the morning dive brings commercial species within range of their demersal trawl nets, so the most favoured timing for a trawl shot at the shelf edge is dawn.

A similar impression of the mid-water nature of the deep scattering layers is provided by an echogram featuring an acoustic mark identified by NSW fishers as being composed of redfish, *Centroberyx affinis* (Plate II). In the echogram made before dawn as the vessel steamed from east to west across the shelf slope towards the shelf (Plate II*A*), the feed layer stretches horizontally just below 200 m. Where the layer intersects with the bottom, the bottom line is particularly thick and intensely red; this shows that the feed layer is on the bottom in 'foul' or untrawlable ground, whereas over the soft bottom the mark is 50–100 m above the bottom. From echograms like this the fishers infer that redfish are found mainly in mid water, but when on the bottom, the redfish prefer reefy bottom to the soft bottom of trawl grounds. The fishers would expect that a trawl shot across the trawlable soft bottom below that mark would catch few redfish 'because the fish are up in the air'. However, if the layer were to drop lower in the water column around dawn and some of it come into contact with the trawlable bottom they would expect redfish to be caught.

In the echogram made before dawn as the vessel steamed north to south parallel to the shelf break (Plate II*B*), the same feed layer is seen to be extensive on a north–south axis, and at a relatively constant height in the water column. Taken together, the echograms show that the feed layer forms a mid-water sheet well clear of the bottom along both an east–west and a north–south axis. Further, the feed layer descends to the bottom along only a relatively narrow strip of the continental slope.

The fishers of the SEF believe that demersal trawls fish only a small part of the SEF ecosystem. Fishers often say that 'the fish go up in the air', into mid water many metres above the bottom, or many kilometres offshore. Demersal trawl nets are only a few metres high. Fishers believe favourable oceanographic and climatic conditions, moon phase, and fish behaviour bring the fish within range of their demersal nets, but that fish spend much of their time foraging elsewhere through the ecosystem where they cannot be fished.

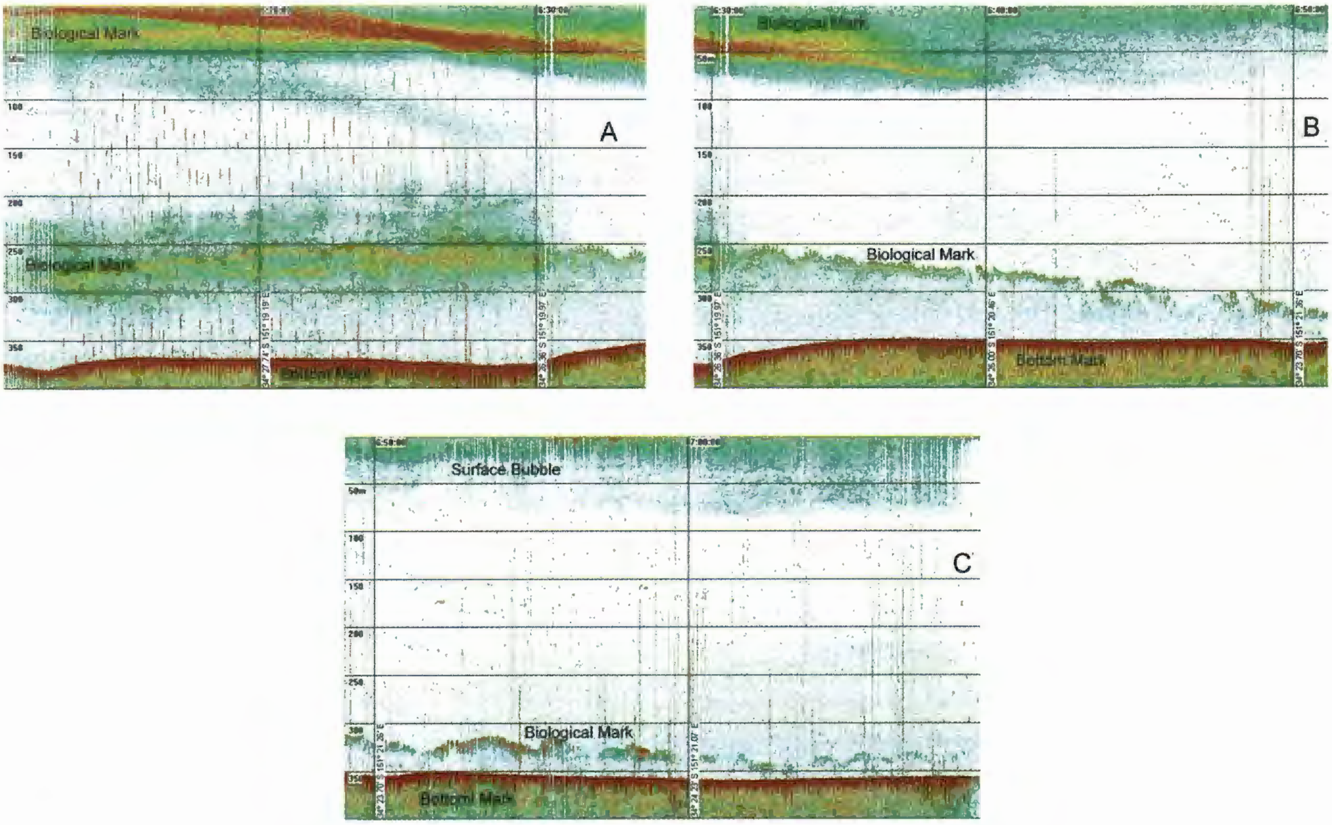


Plate I. Descent of the deep scattering layer, or feed layer, at dawn (0600–0700 hours) to the continental slope off Wollongong, New South Wales, on 14 July 1997. Depth from the surface is given on the left axis. *(A)* Two heavy feed layers, one above 50 m and the other between 200 and 300 m: the deeper seems to receive a 'rain' of marks into it from the surface before both layers concentrate and begin to descend. *(B)* The surface layer fades after having descended to ~100 m but the deeper layer descends to ~350 m, to *(C)* within 50 m of the trawl ground. From Prince *et al.* (1997).

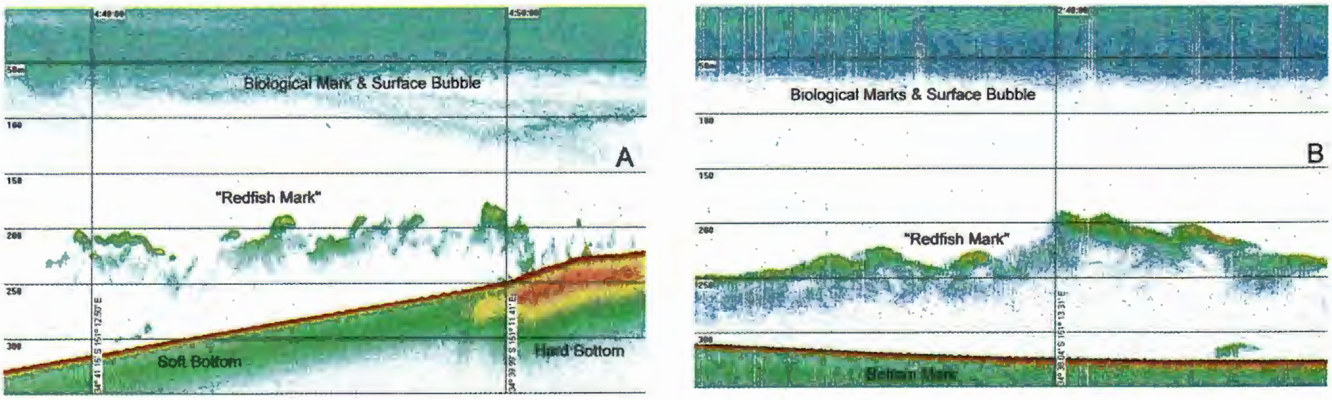


Plate II. Acoustic marks, identified by Ulladulla fishers as redfish, seen before dawn (0200–0400 hours), 28 August 1996. The acoustic layer is seen extending *(A)* east to west [left to right] across the shelf break, and *(B)* north to south [left to right] along the shelf break. From Prince *et al.* (1997).

Trawl grounds

The trawl fishers also emphasize that trawling occurs only over limited areas of the continental shelf, slope and associated seamounts contained within the SEF. Trawl grounds thread between untrawlable reefs along the shelf slope and down the side of seamounts. The same trawl grounds are trawled repeatedly, sometimes even within the same day. During the gemfish season of 1998 one vessel followed precisely the same trawl track during ~15% of its trawl shots over a 6-week period. On one occasion it towed the same track on three consecutive shots within 36 h (Prince *et al.* 1998). During the 1999 gemfish season, three vessels successively trawled the same track four times during a morning, with the final vessel taking the largest catch of gemfish (Prince 1999).

Trawl grounds can only be developed where the underlying substratum is smooth enough not to snag the footline or to rip the belly of the net. Trawl grounds were initially developed on the naturally soft, smooth substrata, but there has been a tendency to develop techniques for trawling more of the previously foul ground.

Today, there are trawl grounds in 200–1000 m scattered throughout the area. However, shallower grounds (<200 m) are still largely restricted to the eastern Bass Strait and off southern NSW where they were originally developed by the NSW Government using Red Funnel Steam Trawlers during the 1920s (Klaer 2001). The only published estimate of the extent of trawl grounds is that, off NSW, ~30% of the shelf-break area was trawlable (Andrew *et al.* 1997). Discussions with fishers and cursory examination of commercial plotter data suggest that this would be an extremely high figure if applied to the SEF in general. Trawling outside NSW began only during the 1980s, and west of Bass Strait the area over which trawling takes place may be <5% of the seabed inside 1000 m.

The restricted extent of trawl grounds limits the species caught, especially west of Bass Strait. The shallow-water assemblage of jackass morwong *Nemadactylus macropterus*, tiger flathead *Neoplatycephalus richardsoni* and john dory *Zeus faber*, an important component of the fishery off NSW, is almost completely unfished west of Bass Strait where there are almost no trawl grounds in <200 m. Blue warehou *Seriolella brama* fishing is significantly curtailed west of Bass Strait for the same reason. Thus, for some species in some areas, observed trends within the fishery may not be indicative of broader regional trends.

Importance of topographical and oceanographic features

The fishers of the SEF believe that topographic and oceanographic features are important influences on catchability. Good fishing conditions are associated with cold currents at depth, and the most productive grounds are clustered around abrupt topography along the shelf break.

Plate III illustrates the coincidence of fish, cold water at depth and topographic feature that is commonly observed by SEF fishers. The two echograms are different views of the same area: Plate III*B* shows a solid mark close to the bottom in 300–350 m, over the high shoulder of the rocky bluff, as the vessel hauled its gear at the end of the morning shot; Plate III*C* shows the bluff itself as the vessel shot away across the feature to the NNE to begin its afternoon shot. The top of the bluff is 300–350 m; visible above it in 250–300 m are several small marks, and below in 350–450 m is seen a larger haze. The haze is probably exaggerated, to some extent, by acoustic echo from the bluff itself. The rocky bluff and fish mark were associated with a temperature anomaly (Plate III*D*); bottom temperatures around the fish mark in Plate III*B* were ~11°C while the surrounding water at that depth was >13°C.

Seasonality and variability

Fishers emphasize the climatically driven variability of the SEF ecosystem. The clear blue and warm waters of the East Australia Current (EAC) and Leeuwin Current (LC) flow along the shelf from the north or north-west respectively, bringing poor catches of most species. In the market fishery, good catches are associated with 'dirty' plankton-rich water associated with deep currents along the shelf edge, or the breakdown of shelf-edge fronts by storm surges. Some fishers of orange roughy *Hoplostethus atlanticus* associate good fishing with cold clear deep-blue 'almost black' water.

Each region displays pronounced seasonality. Vessels large enough to make extended trips away from their home port fish off the east coast of Tasmania during summer but move north to fishing grounds north of Flinders Island during winter. From Bermagui northwards, most of the vessels are too small to make extended trips and they earn the core of their income during winter (Prince *et al.* 1995). A winter flush of cold deep-water currents is associated with seasonal 'runs' of winter-spawning species along the continental shelf, including mirror dory *Zenopsis nebulosus*, john dory, blue grenadier *Macruronus novaezelandiae*, blue and spotted warehou *Seriolella punctata*, morwong, redfish and eastern gemfish. Occasionally, sections of the shelf break off NSW also produce good fishing in summer, but this is less predictable and normally fishing is poor then. West of Bass Strait the main fishing season is also winter, when spawning blue grenadier and warehou are found along the slope. Off Beachport, summer sporadically produces good catches of feeding western gemfish, sub-adult blue grenadier and a scatter of blue eye trevalla *Hyperoglyphe antarctica* across the trawl grounds.

In addition to seasonal variation, fishers emphasize the inter-annual variability of the SEF. From year to year, species composition of catches off any port can vary greatly. For example, during 1995 and 1996 catches of blue warehou off Bermagui grew from <1% to 10–15% of SEF landings,

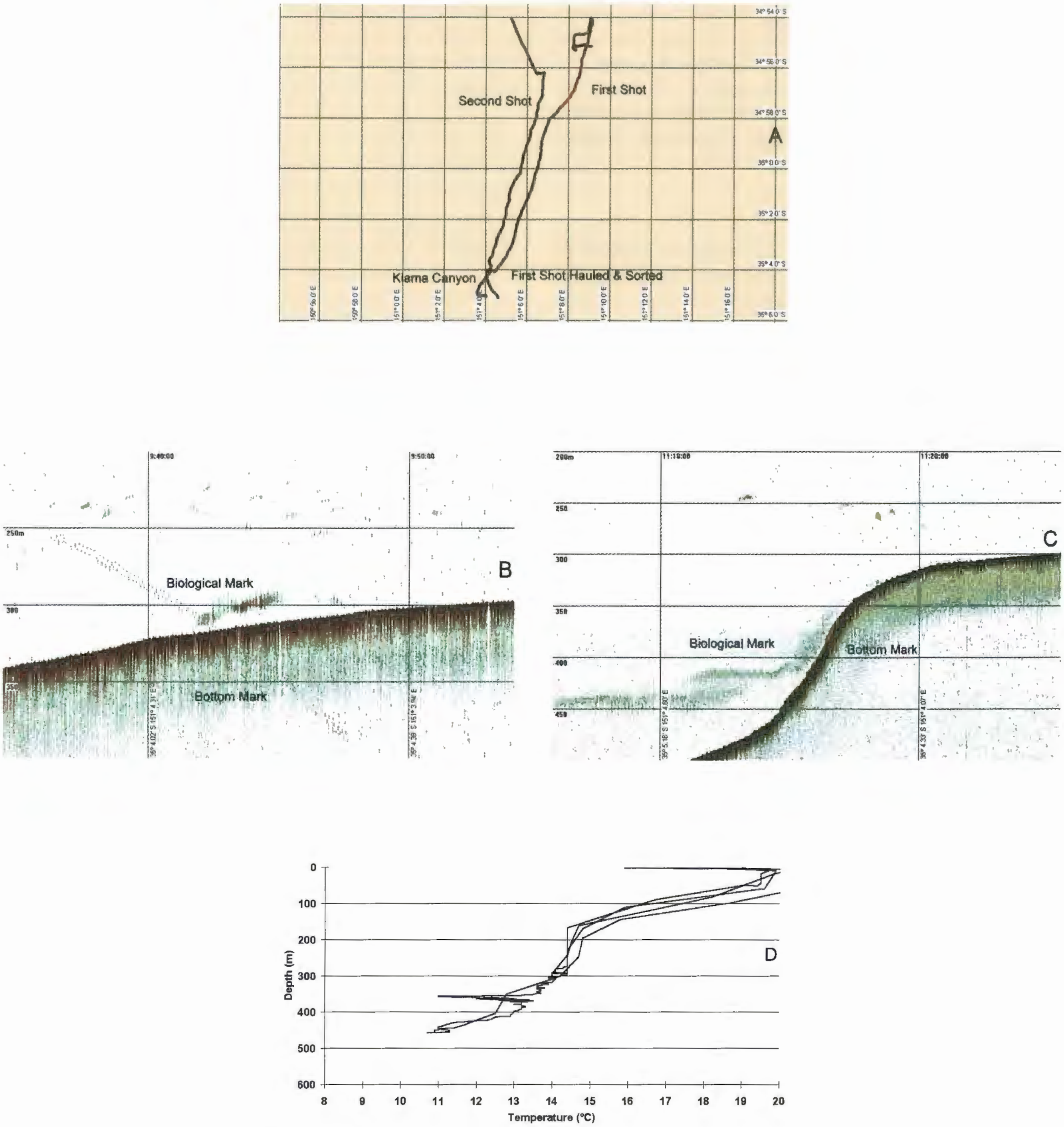


Plate III. *(A)* Track of a trawler on 21 July 1997: at the southern end of the eastern (right) track the net is hauled over a bluff feature, Kiama Canyon, resulting in a series of small zig-zags; the afternoon shot is a smooth line to the west (left) of the morning tow. *(B)* Echogram made as the first shot passed to the shallower side of the bluff; acoustic mark close to the bottom is associated with the shoulder of the bluff. *(C)* Echogram made at the beginning of the afternoon shot, showing the bluff and its associated fish marks around 400–450 m. *(D)* Temperature and depth profile of the two shots showing the 2°C anomaly at the end of the first shot associated with the canyon and fish mark. From Prince *et al.* (1997).

while landings of silver trevally *Pseudocaranx dentex* halved; by 1997 catches of both species had returned to normal. During the same period off Portland, catches of mirror dory, which are normally <5 t, grew to 60–70 t year^{-1} before declining towards normal levels. Fishers regard these types of events as typical of the fishery and have a store of anecdotes about historic variation.

Nutrient enrichment in the SEF

At the base of any ecosystem are nutrients supporting primary productivity. The major sources of nutrients to the SEF are deep-oceanic Sub Antarctic Waters (SAW) (Godfrey *et al.* 1980; Gibbs *et al.* 1986*a*; Harris *et al.* 1987, 1991). These are mixed into the euphotic zone along the Sub Tropical Convergence (STC) that stretches across the Tasman Sea to the east of Tasmania, and along the South Australian shelf break to the west of Tasmania (Deacon 1982). To the east of Tasmania, SAW mixes with the south-flowing warm surface waters of the EAC, to the west with the LC (Cresswell *et al.* 1994).

The entire circumpolar STC is an extensive region of enhanced oceanic productivity (Marshall 1979). Enriched phytoplankton production characterizes the STC across the Tasman Sea (Plate IV) and is also seen around the continental shelves of Australia and New Zealand and prominent underwater features such as the Chatham Rise. Within the STC, marine productivity is an order of magnitude higher along the edge of the continental shelf, where a range of factors intensifies the upward mixing of SAW (Cresswell 1994; Young *et al.* 1996).

Deepwater currents

Coastal flows along the edge of the continental shelf set up deeper cold counter currents (Scott 1981; Pearce and Boland 1982; Huyer *et al.* 1988) which, together with the deep westerly drift of bottom waters, sporadically drive SAW up the slope. Counter currents are commonly generated around the point at which the EAC and LC detach from the continental shelf, and around the base of the warm core eddies formed by the two warm coastal currents (Tranter *et al.* 1980, 1983).

Alongshore continental winds

Continental winds blowing parallel to the shore can drive upwelling along the shelf break during summer off the Bonney Coast and Lakes Entrance (Lewis 1981; Schahinger 1987; Bax and Williams 2000).

Abrupt topographical features

Abrupt underwater topographical features such as the shelf break itself, but particularly canyons, promontories, bluffs and seamounts, interrupt flows of oceanic water and cause turbulence that transports bottom waters towards the surface (Marshall 1979). In many parts of the SEF, canyons and promontories apparently channel upwelling water onto the shelf (Rochford 1972, 1975, 1977*a*; Lewis 1981). Downwelling flows of coastal waters may also seasonally reverse the flow through these structures (Tomczak 1985).

Winter overturn

At the edge of the continental shelf, temperature and density fronts usually separate nutrient-poor coastal and shelf waters from oceanic waters carrying SAW. However, throughout temperate and subpolar waters surface waters tend to cool during winter, increasing their density and causing them to sink. This forms convective currents that break down the shelf-edge fronts and bring deeper nutrient-rich water up into the euphotic zone (Marshall 1979). In the SEF the importance of this winter overturn is enhanced by two factors as follows.

(i) The density of coastal and shelf waters. Coastal waters move eastwards through the SEF driven by westerly winds. Their original source in the evaporative shallows of the Great Australian Bight and the South Australian gulfs make the coastal flow more saline than adjacent oceanic waters (Boland 1971; Gibbs *et al.* 1986*a*, 1986*b*, 1991). Winter cooling enhances the difference in density between the coastal and oceanic waters and produces pronounced downwelling in some areas. Although generally associated with low nutrient regimes, downwelling of coastal waters in the context of the SEF may play an important role in breaking down shelf-edge fronts and displacing deeper oceanic water, pushing relatively nutrient-rich water towards the photic zone (Gibbs *et al.* 1986*a*, 1986*b*, 1991).

(ii) Winter winds mixing the surface layer. Probably the most important factor enhancing the winter overturn is the mixing of surface layers by strong westerly winds associated with the cold fronts of winter storm events (Harris *et al.* 1987).

The SEF ecosystem

Hotspots of productivity

The conjunction of oceanographic and topographic features creates hotspots of fisheries productivity around south-eastern Australia and drives the seasonal variability of the ecosystem. The key fishing grounds for all the main commercial shelf-based marine fisheries (abalone, lobster, scallops, shark, squid, prawn, tuna and other fin-fish) are clustered around the same hotspots. Off New Zealand, similar hotspots of fisheries production are also hotspots for biodiversity (McClatchie *et al.* 1995).

Starting from the west, the key regions of fisheries production and the key parameters that drive them are as follows.

The Bonney Coast between Kangaroo Island and Portland

Schahinger (1987) noted the diversity of oceanographic phenomena both on and off the shelf through this region.

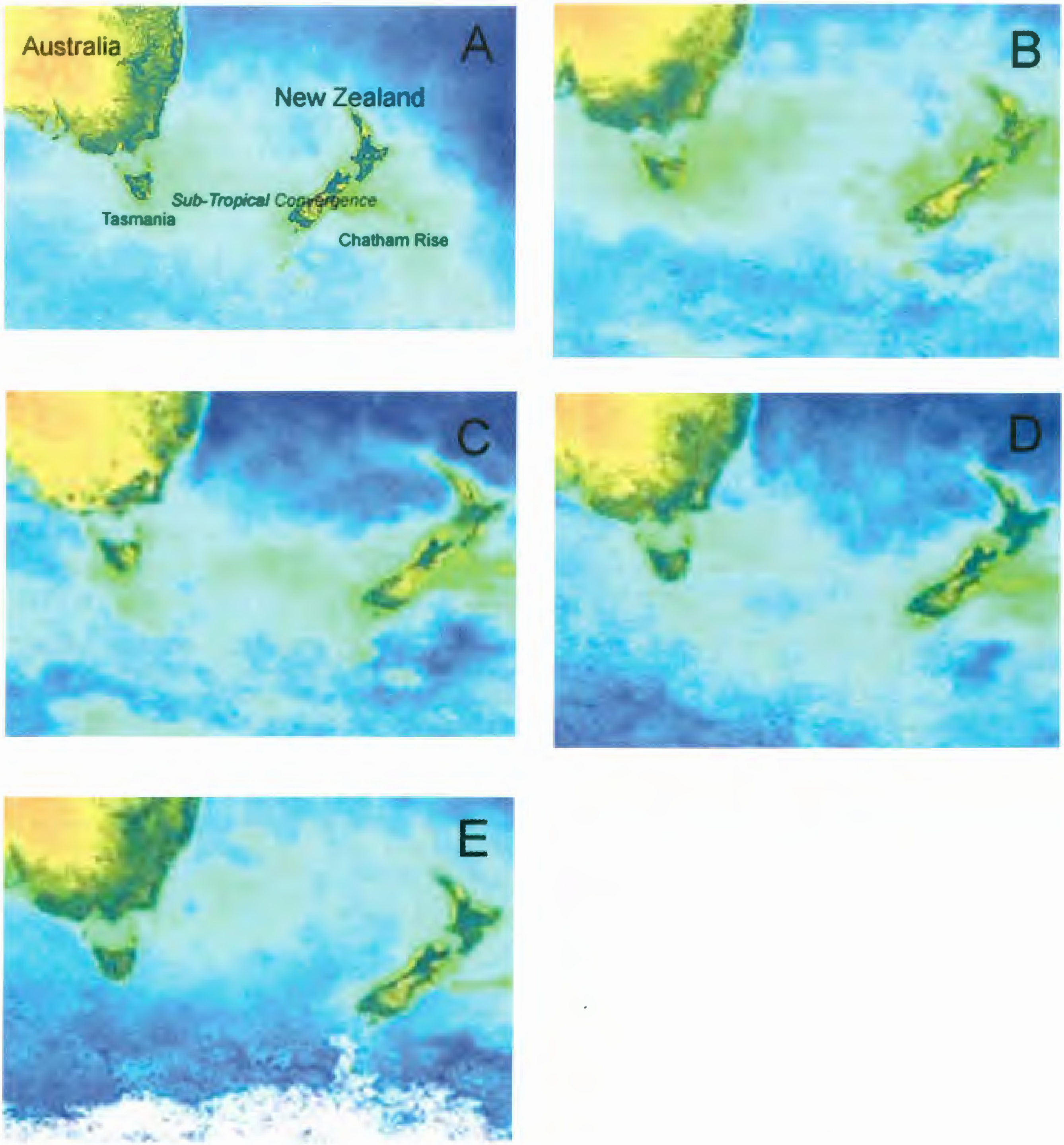


Plate IV. Ocean colour data showing surface phytoplankton concentrations, September 1997 to July 1998: *(A)* Band of concentrated phytoplankton shows region of Sub-Tropical Convergence. *(B–E)* Quarterly images for the same period, depicting annual north–south oscillation of the convergence zone: *(B)* September–November; *(C)* December–February; *(D)* March–May; *(E)* June–August. (Images provided by the SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE.)

The shelf is sporadically enriched in summer by upwelling events associated with canyons and driven by south-easterly winds (Hynd and Robins 1967; Rochford 1977*b*; Lewis 1981; Schahinger 1987). During winter the cooling west-flowing shelf waters have a tendency to subside down the continental shelf, but strong westerly storm winds can break up the downwelling shelf fronts and drive enriched oceanic water onto the shelf (Schahinger 1987).

Western Tasmania from King Island to Maatsuyker Island

The western shelf edge of Tasmania from King Island to Maatsuyker Island is the least-studied area of the SEF. However, shelf-edge productivity is apparently derived principally from winter mixing of the shelf-edge front (Godfrey *et al.* 1980; Gibbs *et al.* 1986*a*). This will be enhanced by the strong westerly winds of winter storms. At the northern and southern margins of the Tasmanian west coast, hotspots of fisheries production are associated with the canyons off King Island and the Maatsuyker seamounts. As in other areas, these topographic features probably interact with downwelling shelf water, the Zeehan Current in this region, and deeper currents to enhance mixing rates and advect oceanic water onto the shelf.

Eastern Tasmania

The hydrography of eastern Tasmania is also complex, with warm filaments and eddies of the EAC meeting cold SAW (Young *et al.* 1996). On the shelf, apart from the periodic intrusions of EAC water, a generally northward flow of SAW mixed with west-coast water of the Zeehan Current and river runoff produces a tongue of cold nutrient-rich water that can extend the length of the island (Young *et al.* 1996). Along the slope of eastern Tasmania a string of extinct volcanoes forms seamounts, including St Helen's Hill, that enhance the mixing of oceanic and shelf waters. The influence of SAW is strongest in this region during winter when the main flow of the EAC retreats to the north (Ridgway and Godfrey 1997), and winter storms break down shelf-edge fronts (Harris *et al.* 1991). During summer, the currents associated with the separation of the EAC from the shelf and its resulting eddy field provide the ecosystem in the region with both warmth and nutrients.

The winter influence of the SAW sets the production base for the following summer in this region, but low temperature and light intensities limit productivity during winter (Harris *et al.* 1991). Strong westerly winds break down shelf-edge fronts, and in years of more wind the spring bloom off south-eastern Tasmania can be first delayed and then extended by up to three months, thereby increasing 'new' primary production by an order of magnitude (Harris *et al.* 1991).

Eastern Bass Strait

Flinders Island to Eden is the least seasonal region of the fishery, with enrichment of shelf ecosystems possible at any time of the year. Summer upwelling may occur through the region (Newell 1961), driven by summer winds and augmented by counter currents around warm core eddies or the detachment point of the EAC that interact with the canyon systems off Lakes Entrance, Deal Island and Banks Strait (Rochford 1977*a*).

The effect of the winter overturn in this region is augmented by a range of factors including the following. *(i)* The Bass Strait Cascade; in some years downwelling of dense east-flowing water at the eastern extremity of Bass Strait enhances mixing along the shelf-edge front (Gibbs *et al.* 1986*b*) especially around the canyon systems off Lakes Entrance (Tomczak 1985). *(ii)* Strong storm winds that break down shelf-edge fronts. *(iii)* Currents around warm core eddies that may, during winter, drive deeper waters inshore (Godfrey *et al.* 1980).

North of Cape Howe

Counter currents around where the main body of the EAC detaches from the shelf seasonally enrich the shelf edge during winter. Currents around warm core eddies can augment winter upwelling. Southerly storms breaking down the shelf-edge front, and northerly winds blowing parallel to the coast, may also augment the upward mixing of SAW during winter. Most of these factors can also lead to enrichment of this region during summer, but summer phytoplankton blooms are generally less dense and less regular (Hallegraeff and Jeffrey 1993). Upwelling coincides with a series of canyons (Rochford 1972, 1975, 1977*a*).

Food chain

Young *et al.* (1996) studied the biomass of zooplankton and micronekton communities of the fishing grounds for southern bluefin tuna *Thunnus maccoyii* off eastern Tasmania with mid-water trawls during 1992–94. They sampled shelf waters of Tasmania, sub-tropical waters of the EAC, cooler SAW and the frontal waters of the STC between the EAC and SAW. The biomass was dominated by four broad taxa: gelatinous zooplankton, crustaceans, mesopelagic planktivorous fish and squid.

Gelatinous zooplankton

Gelatinous zooplankters are similar in density to water, so are not readily detected acoustically. Mid-water trawling destroys their structure, so quantitative study is almost impossible (Marshall 1979). Only recently have remote-control submersible vehicles permitted *in situ* studies of the behaviour and role of gelatinous zooplankton (Robison 1995).

Oceanic mid waters in many regions contain highly dynamic ecosystems structured by the ephemeral growth of gelatinous zooplankton (Robison 1995; Pagès *et al.* 1996). Such species have short regeneration times, and under favourable conditions their communities can increase in abundance over time scales of weeks and months (Kashkina 1986). Many species of gelatinous zooplankton exhibit diel vertical migrations (Pugh 1984; Robison 1995).

Pakhomov *et al.* (1994) found gelatinous zooplankton in the STC around South Africa to constitute 90% of the biomass in surface waters during the day, but just 50% of the biomass during the night when vertically migrating fish species re-entered the surface waters. Pelagic tunicates and coelenterates are voracious consumers of phyto- and zooplankton, in some cases being the major predator of plankton (Purcell 1992; Mills 1995). In Sub-Antarctic ecosystems, filter-feeding gelatinous zooplankton may compete directly for the same food resource as krill (Pagès *et al.* 1996). Low abundances of krill coincide with high abundances of feeding pelagic tunicates, so high abundances of pelagic tunicates perhaps depress krill recruitment (Siegel and Loeb 1995; Pagès *et al.* 1996).

The gelatinous zooplankton over the slope off southern Tasmania represented 60% of the overall wet biomass sampled with pelagic trawls, primarily the pyrosome *Pryosoma atlanticum* (56%) and the salp *Thetys vagina* (29%), but may be a relatively unimportant source of production because its carbon content is low: 0.3% compared with 16.5% in migrating fishes (Williams and Koslow 1997).

Many researchers have dismissed the importance of this biomass in pelagic ecosystems because of its high water content (90–97%) and the apparent avoidance of salp concentrations by many fish species (Kashkina 1986; Pagès *et al.* 1996). However, as argued by Pagès *et al.* (1996), recent studies show that excretion and respiration rates of gelatinous zooplankton are in the same range as those of non-gelatinous zooplankton if carbon content is used as a unit of body mass. Although the carbon content of the tissues is low, the amount of carbon passing through the gut is high. Much of the carbon content of a salp resides in the phyto- and zooplankton packed into its stomach (Kashkina 1986). Adding to their calorific value, many salps contain hyperiid amphipods living as parasites and symbionts (Harbison *et al.* 1977).

Gelatinous zooplankton is preyed on by a wide array of species (Pagès *et al.* 1996), including albatrosses and pintado pigeons (*Daption capense*) and many species of crustaceans. It is important in the diets of fish around the world (Kashkina 1986), although there is evidence that it is not the preferred diet of some species (Huntley *et al.* 1989). Many predators of gelatinous zooplankters do not eat them indiscriminately but may target their stomachs with the concentrated pellets of phyto- and zooplankton, or the associated hyperiid amphipods, and only incidentally ingest the membranes containing relatively indigestible mucopolysaccharides (Kashkina 1986).

Kashkina (1986) noted the significance of salp to fish communities in the south-western Pacific. Over the Chatham Rise, Kashkina (1986) repeatedly recorded vigorous development of tunicates, reaching up to 99.6% of the plankton in the waters of the continental slope and deep-sea zones. Over the seamounts of the Tasman Sea and along the east coast of southern New Zealand, most of the fish biomass seasonally switched to feeding extensively on gelatinous zooplankton. Kashkina (1986) concluded that salps and pyrosomes are of maximum importance in the diets of the main species of the Tasman Sea and Chatham Rise: blue grenadier, blue warehou, orange roughy, banded whiptail (*Coelorinchus fasciatus*), gargoyle fish (*Coelorinchus mirus*) and toothed whiptail (*Lepidorhynchus denticulatus*). They were also the principal food of spotted warehou, spiky dory (*Neocyttus rhomboidalis*), warty oreo (*Allocyttus verrucosus*), ocean perch (*Helicolenus percoides*) and silverside (*Argentina australiae*). Kashkina (1986) concluded that the New Zealand region was one of the few areas in the world where tunicates and coelenterates together with their associated crustaceans form the main components at the base of the food chain.

In their study of the diet of 15 SEF species caught by demersal and mid-water trawling over the slope off Maria I. in southern Tasmania, Blaber and Bulman (1987) found the pyrosome *Pyrosoma atlanticum* to be the most important food item in the diet of ocean perch. In contrast, Young *et al.* (1996) concluded that along with krill in shelf waters, gelatinous zooplankton played a major role in the SEF ecosystem, by gathering and storing energy from the primary production of phytoplankton blooms and then, as prey, passing energy up the food chain. Gelatinous zooplankton was found in the stomachs of southern bluefin tuna and its principal prey species, such as jack mackerel. Young *et al.* (1996) suggested that offshore, where the role of crustaceans in pelagic food chains is reduced, the importance of gelatinous zooplankton in linking primary and secondary levels of production may be even greater than in shelf waters.

Crustaceans

Young et al. (1996) observed that offshore the crustaceans were a range of decapods and several euphausiids. Hyperiid amphipods living in salps are prominent in the diet of offshore-caught southern bluefin tuna off south-eastern Tasmania (Young et al. 1997).

On the shelf the euphausiid *Nyctiphanes australis*, locally called krill, dominates research catches of crustaceans (Young *et al.* 1996); it grazes on phytoplankton and is the major component of the zooplankton community in coastal waters of south-eastern Australia (Nyan Taw and Ritz 1979; Blackburn 1980; Ritz and Hosie 1982; Young *et al.* 1993). The importance of krill in the ecosystem of shelf waters of southern Australia has been recognized since Blackburn (1957) found it to be the principal prey item of barracouta *Thyrsites atun* through the Bass Strait. In south-eastern Australia, krill is important in the diet of a wide range of predators over the continental shelf (Blackburn 1980; Ritz and Hosie 1982; Young *et al.* 1993): southern bluefin tuna, skipjack tuna *Katsuwonus pelamis*, Australian salmon *Arripis trutta*, tiger flathead, jack mackerel and mutton birds *Puffinus tenuirostris*.

In their study of the diet of 15 SEF species caught by demersal and mid-water trawling over the continental slope off Maria I., Blaber and Bulman (1987) found krill to be the most important food of toothed whiptails, big-eyed cardinalfish *Epigonus lenimen* and the white cardinalfish *E. denticulatus*. Other species such as southern frostfish, for which krill was generally less important, switched to feeding predominantly on krill during periods of its peak abundance over summer.

Squid

Squid are also thought to form an important link in oceanic food chains (Clarke 1966; Zuev and Nesis 1971) but less is known about their distribution and ecology than is known about fish, partly because squid are highly mobile and consequently almost unrepresented in trawl catches, they also reflect acoustic signals poorly. Data on oceanic squid in the Tasman Sea are notably scant (Brandt 1981) and there are even fewer data for the rest of the SEF area. On the basis of depth-stratified catch rates to the east and west of Bass Strait, Nowara and Walker (1997) concluded that populations of Gould's squid (*Nototodarus gouldi*) exhibit diel vertical migrations and that small individuals tend to rise higher in the water column at night than larger ones.

Mesopelagic planktivorous fish

Another important component at the base of the SEF food chain is a broad group of small mid-water (meso-pelagic) fish with teeth specifically adapted for plucking differing types of zooplankton from the water column. Broadly speaking, meso-pelagic planktivores spend the day in depths >200 m and may be oceanic or merely neritic. They are found in all oceans but their productivity and densities are generally highest in subtropical and tropical seas (Clark 1973, 1978; Gjøsaeter and Kawaguchi 1980). Meso-pelagic fish assemblages can be broadly grouped as either vertical migrators, which includes most myctophids (lantern fish) and their stomiatoid predators, or non-migrating, such as sternoptychids, and *Cyclothone* spp. The migrators feed primarily at night on the productivity of the euphotic zone in epi-pelagic or surface waters (<200 m), whereas the non-migrators feed during the day, laying ambush to the migrators at depth (Clark 1973, 1978; Robison 1995).

Boden and Kampa (1967) were the first to propose that the vertical migration of mid-water species is a response to light intensity in the water column. It is now generally accepted that, to minimize predation, mid-water species live permanently in almost total darkness, only foraging up towards the photic zone under cover of darkness. Not all species migrate vertically, and even within migrating species not all individuals migrate vertically every night. Usually, a residual part of the population remains at depth during the night (Tucker 1951; Paxton 1967; Clark 1973). This may be due to differing behaviour among individuals or because satiated individuals do not need to forage up through the water column (Pearcy *et al.* 1977). Many mid-water species, especially congeners of similar size, show some vertical separation during the day (Clark 1978), although there can be considerable overlap. However, at night many vertical migrators will feed in the same depth interval (0–200 m), although many species feed selectively, usually by size category, with smaller animals feeding at shallower depths than larger animals (Clark 1978).

Off the southern NSW coast, across a warm core eddy that had broken away from the EAC, 88% of the total catch of a mid-water trawl was myctophids, with seven species constituting 86% of the myctophid catch (Brandt 1981); the recording of more species at night than during the day showed the importance of diurnal vertical migrations in the assemblage studied.

Over the mid slope of southern Tasmania, fish contributed 89% of the micronekton biomass captured (excluding gelatinous zooplankton) and 135 of 178 species (Williams and Koslow 1997). In turn, the fish component was dominated (48% of catch) by myctophids. During the day, most of the biomass was below 400 m, with a peak at 400–525 m and a second peak at 775–900 m, and the biomass in the surface 0–300 m was negligible (<0.2% of the observable biomass above 1000 m). At night, the surface 0–300 m contained 53% of the biomass, with ~20% of the biomass in each of the 0–100 m and 100–200 m strata. Among the 20 dominant fish were four patterns of diel vertical migration: nycto-epipelagic moving out of deep water into shallow (eight species), partial movements (five species), no vertical migration (six species), and one lower mesopelagic that dispersed throughout the depth range rather than migrating to the surface (Williams and Koslow 1997).

Over the shelf break and on the slope near Maria I., the myctophid *Lampanyctodes hectoris* constituted >90% of the fish biomass (May and Blaber 1989). As noted by Young *et al.* (1993), the summer densities of *L. hectoris* detected by May and Blaber (1989), ~390 g m^{-2}, were extremely high compared with global estimates of 0.1–6.5g m^{-2} (Gjøsaeter and Kawaguchi 1980). Young *et al.* (1993) found *L. hectoris* to be restricted to a thin band along the continental slope over waters 300–500 m deep.

Blaber and Bulman (1987) described the importance of *L. hectoris* to SEF species near Maria I. and its importance in the diet of the 15 major species in their trawl samples. Among the pelagic piscivores they studied, lanternfish were the principal diet of the blue grenadier, Ray's bream *Brama brama* and the three-spined cardinal fish *Apogonops anomalus*. Both jack mackerel and southern frostfish switched opportunistically to lanternfish during seasonal abundances. Lanternfish were also a significant component in the diet of species that Blaber and Bulman (1987) categorized as benthopelagic, including ocean perch, king dory (*Cyttus traversi*), toothed whiptail, spiky dory, big-eyed cardinalfish species, ling (*Genypterus blacodes*) and brier shark (*Deania calcea*). Even epibenthic invertebrate feeders such as the banded bellowfish (*Centriscops humerosis*) and whiptails (*Coelorinchus* spp.) were found to supplement their diet seasonally with lantern fish.

Other SEF fish

May and Blaber (1989) found jack mackerel to constitute 2% of the fish biomass over the continental slope near Maria I. — after *L. hectoris* the second most abundant pelagic species in their samples. They categorized jack mackerel as an omnivorous piscivore. Jack mackerel apparently feed through the water column, forming feeding schools around surface swarms of krill during daylight in some seasons, and migrating diurnally through the water column at other times (Young et al. 1993). Jack mackerel are an important prey species for the higher piscivores of the SEF, including gemfish, southern frostfish and southern bluefin tuna (Prince 1996; Young et al. 1997).

Blaber and Bulman (1987) categorized the fish of the SEF into four trophic levels:

- Pelagic piscivores, including jack mackerel, Ray's bream, three-spined cardinal fish, southern frostfish and blue grenadier, which feed principally on the lanternfish *L. hectoris*.
- Epibenthic piscivores, such as brier shark and ling, which consume a wide range of fish species.
- Consumers of epibenthic invertebrates, such as other whiptails and the banded bellowsfish, which feed mainly on benthic crustaceans and ophiuroids but supplement their diet with lanternfish.
- Benthopelagic omnivores such as king dory, some whiptails including the toothed whiptail, spiky dory, ocean perch, and white and big-eyed cardinalfish, which feed on a wide range of prey including lanternfish and gelatinous zooplankton. Blaber and Bulman (1987) noted that the extent to which members of this class ascend the water column to feed is unclear.

A broader description of the fauna of the SEF ecosystem was developed after >230 species were sampled with a wide range of commercial and research sampling methods applied across all habitat types (Bax *et al.* 1999); 114 of the species selected as representative of the SEF faunal assemblage were grouped into 20 ecomorphotypes based on mode of locomotion, feeding and adaptation for self preservation. Bax *et al.* (1999) identified four demersal ecomorphotypes comprising 18 species with dorsoventrally flattened bodies for living on the seabed; they are crushers of benthic infauna and include elasmobranchs from the families Rajidae (rays), Rhinobatidae (skates), Hypnidae and Squatinidae (angel shark), and teleosts from the Pleuronectidae (flounders) and Bothidae. At the pelagic extreme of the faunal assemblage were three ecomorphotypes containing at least 15 mobile opportunistic piscivorous species, all higher-order predators in the SEF system; Bax *et al.* (1999) classed these as cruising ram feeders, and they include pelagic elasmobranchs from the families Triakidae, Sphyrnidae and Squalidae, and teleosts from the Scombridae (jack mackerel), Carangidae (trevally), and Gempylidae (gemfish, frostfish, oilfish); while clearly adapted for pelagic foraging, many of these teleosts are also adapted for some degree of demersal suction feeding. Between these two extremes are 13 ecomorphotypes comprising some 80 species that, to varying degrees, rely on both benthic and pelagic habitats. The biggest group of these, 7 ecomorphotypes with 46 species, are oscillatory manoeuvrers – species that maintain neutral bouyancy while they hover slowly into close range of their prey with small sculling strokes of either caudal or pectoral fins. Approximately 20 of these species, pufferfish (Diodontidae and Tetraodontidae), boxfish (Aracanidae), leather jackets (Monacanthidae), morwong (Cheilodactylidae) or bellowsfish (Macroramphosidae), clearly live demersally and feed by probing, biting, and crushing benthic infauna. However, the remaining species show some level of adaptation for pelagic foraging. This group also includes some pufferfish and leatherjackets, but also 5 species of dories (Zeidae), whose thin profile, colouration and protusible suction-action mouths adapt them for feeding on mesopelagic prey in low light intensities. Also in this group are 25 species of larger opportunistic predators such as redfish (Berycidae), hapuka (Serranidae) and ocean perch (Scorpaenidae) with powerful tails and large mouths suitable for both ram and suction feeding in either demersal or pelagic environments. Bax *et al.* (1999) described a final group of four ecomorphotypes with some 28 species that were adapted for benthic living and demersal suction feeding: lancets (Triglidae), whiptails (Macrouridae), flathead (Platycephalidae) and ling (Moridae). The body of many of these has some degree of dorsoventral flattening, and fin arrangements suggest adaptation to life on the seabed. However, these species are also adapted for some level of pelagic ram feeding.

Thus we glimpse the diversity of the SEF fish fauna together with the degree the species mix both pelagic and demersal feeding strategies.

Bax and Williams (2000) found that, although benthic sources of prey dominated across 70 fish species in the SEF region, the prey of most SEF quota species is pelagic. Stable isotopes showed that marine phytoplankton provides the basic nutrients for both benthic and pelagic components of the SEF ecosystem. They concluded that fisheries production is principally driven by direct pelagic production, while a more diverse, but less abundant, demersal fish fauna is supported by indirect pelagic production cycled through the benthos.

Robison (1995) used submersibles to observe fish foraging pelagically through the mid-water environment. Down to 1000 m, visual feeding remains the dominant mode of hunting. He has observed that the fish typically forage upwards under conditions of declining light intensity, and may spend most of their time orientated vertically rather than horizontally. Almost universally they hunt by silhouetting their prey against low intensities of surface illumination, approaching stealthily from below under cover of even lower intensities of light. In common with many SEF species, mid-water species typically have forward-pointing mouths and eyes for hunting prey in front and above them. They are shaped, coloured and counter-shaded to reduce their visibility when they approach from below under low light intensities, and to protect them in turn from being silhouetted from below. They possess well developed lateral lines, which increase their ability to hunt prey and avoid predators in near darkness.

In support of the importance among these species of foraging upwards through the water column, Hoverkamp (1989) observed euphausiids to be nine times more vulnerable to nets dropped from above than from below. This seemingly demonstrates strong adaptation in krill against predators approaching from below.

Seasonality and variability in the SEF

The fisher lore about the importance of oceanographic and topographical features and the environmental variability of the SEF seems well founded.

As observed in other parts of the world (see Cushing 1982), seasonal and interannual variations in the movement of water masses profoundly affect nutrient cycling and structure of the food chain in the SEF (Harris *et al.* 1991). Nutrient-rich SAW increases the flow of nutrients into predominantly temperate SEF food chains, and the EAC and LC bring intrusions of oligotrophic water and influxes of subtropical species (Harris *et al.* 1987; May and Blaber 1989; Young *et al.* 1993, 1996).

Seasonal and interannual cycling in the SEF has mostly been studied to the east of Bass Strait and so the discussion must focus on that region. The same processes also occur to the west, but possibly with different and more complex timing. East of Bass Strait, the influence of the EAC is strongest during summer (Ridgway and Godfrey 1997). The EAC separates from the continental shelf around Cape Howe (38–40°S), and its eddy field and thus the STC lies adjacent to the east coast of Tasmania. During autumn, the Tasman Sea across the broad region of the STC supports a dispersed phytoplankton bloom (Plate IV*D*). The influence of SAW is strongest during winter when the separation point of the EAC is pushed northward to southern NSW (30–34°S). During late winter and early spring a second seasonal bloom occurs across the STC adjacent to the south coast of NSW (Plate IV*B*).

Overlaid on this seasonal cycle there is considerable meteorology-driven variability in the position of the STC between years (Harris *et al.* 1988). Besides determining the extent to which the STC migrates northwards and southwards each season, regional meteorology also influences the strength and direction of coastal winds, rates of surface mixing, and the extent of winter overturn at shelf-edge fronts.

The El Niño–Southern Oscillation phenomenon (ENSO) is strongly linked to the strength and number of cold storm fronts and low-pressure systems that seasonally influence the SEF. The ENSO is also linked to the latitude of the continental high-pressure system that characteristically dominates southern Australian meteorological conditions (Harris *et al.* 1988, 1991). Intrusions of warm water into cooler regions and a decrease in wind mixing results during periods of El Niño in lower productivity at the base of the SEF food chain, whereas La Niña events seem to coincide with high rates of mixing through the water column and pulses of relative enrichment for the SEF.

Species composition

Many myctophids undergo seasonal changes in abundance off eastern Australia; Brandt (1981) attributed this to the transport of subtropical species in flows of EAC water.

May and Blaber (1989) observed a five-fold increase in the biomass of pelagic and dispersed species off Maria I. during summer, and a doubling of benthic species. The most variable pelagic species increased 200-fold, and blue grenadier and the lantern fish *L. hectoris* increased 10-fold. May and Blaber (1989) hypothesized that aggregations of *L. hectoris* follow the seasonal north–south cycling of the EAC and that mobile predatory species (e.g. blue grenadier, Ray's bream, toothed whiptails, jack mackerel) followed the myctophids.

Young *et al.* (1993) observed the density of adult krill undergoing seasonal and interannual cycles off eastern Tasmania. Densities increased during the autumn and spring phytoplankton blooms, whereas the seasonal intrusion of EAC water reduced sampled densities. Overlying the seasonal cycle were interannual variations driven by the same oceanographic phenomena. Sampled krill density was two orders of magnitude lower in 1989 than in 1990 or 1991 following the 1990 La Niña event. The availability of jack mackerel to the purse-seine fishery off south-eastern Tasmania tracked the seasonal density of krill (Young *et al.* 1993).

Young *et al.* (1996) documented a progressive increase in the total biomass of zooplankton off south-eastern Tasmania during 1992–94 attributable to the increased influence of SAW through that period. Biomass increased primarily through growth and reproduction of gelatinous zooplankton, which by 1994 dominated in the surface 200 m and represented >90% of the biomass in the surface 100 m.

Recruitment

Thresher *et al.* (1989) observed recruitment of a small reef fish to coincide with periodic algal blooms in Storm Bay. Invoking Cushing's (1982) match/mismatch hypothesis, they supposed that phytoplankton blooms enhance the survival of larvae. The importance of matching egg and larval production with the timing and location of phytoplankton blooms is also suggested by Prince *et al.* (1997, 1998) who observed breeding aggregations of eastern gemfish to coincide with ephemeral plumes of SAW along the NSW shelf.

This being the case we might expect recruitment trends for many SEF species to be linked with climatic and oceanographic variability. Agreed assessments have now been developed by the South East Fisheries Assessment Group for orange roughy, eastern gemfish, blue warehou and blue grenadier, and all suggest some level of environmental variability in recruitment. The La Niña conditions of 1996 which, as discussed above, coincided with varying catch compositions off Bermagui and Portland, also caused positive anomalies in the recruitment of eastern gemfish, blue warehou and blue grenadier. Anecdotal accounts also suggest that they produced pulses of recruitment for southern rock lobster *Jasus edwardsii*, scallops, snapper and barracouta.

The primary productivity at the base of the SEF food chain (phytoplankton and gelatinous zooplankton) has regeneration times measured in weeks and months. Thus, the density of a plankton bloom can build over a short time purely through the processes of growth and reproduction (Kashkina 1986; Young *et al.* 1996), but this is not true for the higher trophic levels. Populations of krill, myctophids, jack mackerel and higher-order predators consist of multiple year classes (Ritz and Hosie 1982; Young *et al.* 1993). The effect of recruitment variability on the biomass of these species will lag by several years and cannot explain the short-term seasonal and interannual variability in population densities described by Brandt (1981), May and Blaber (1989) and Young *et al.* (1993).

Catchability

Short-term variations in density observed for the species higher in the SEF food chain must result from changes in catchability. The question that arises is, how catchability varies to this degree.

There is probably no single answer; we are considering a wide range of species with differing biology, morphology and mobility. Blackburn (1957), May and Blaber (1989) and Young (1998) suggest that the most mobile predators of the SEF, such as southern bluefin tuna, barracouta, jack mackerel, blue grenadier and Ray's bream, move in and out of regions following aggregations of their prey.

However, virtually all SEF species display considerable variations in catchability and it seems unlikely that the less mobile species, such as krill, ocean perch, tiger flathead and ling, move between regions. It is more likely that, amongst these species, catchability is related largely to their degree of aggregation around concentrations of prey, becoming highly catchable when prey are aggregated and relatively uncatchable when foraging on dispersed food sources. Blackburn (1980), apparently supported by Young *et al.* (1993), suggests this mechanism to explain variations in sampled density of krill off south-eastern Tasmania. These authors postulate that the catchability of adult krill in mid-water nets increased when they formed feeding swarms in response to phytoplankton blooms and declined when the blooms dispersed.

Where variation in catchability through aggregation and dispersal is invoked, we should expect that a decrease in density observed through scientific sampling or commercial catch rates would be compensated by a corresponding increase in the area being used by the population. An observation concerning krill (Young 1998) supports this; although krill are normally confined to the shelf, when sampled density declined during 1989 they extended their distribution offshore.

Importance of the shelf

Until relatively recently, the implicit scientific view of the SEF has been that the benthic shelf and slope environment constitutes most of the ecosystem being used by the fish stocks of the SEF and that the principally demersal species are restricted to ribbon-like distributions within narrow depth bands (Tilzey 1994).

By contrast, fishers emphasize the oceanic and extensive nature of the SEF stocks. In the past, these views were often the basis for fishers to claim that there were large oceanic, or otherwise cryptic, reserves of biomass, and thus to argue against further management restrictions. Clearly, reality lies between these two poles, and both sides of this discussion are rapidly converging. But then what is the importance of the shelf break to these fisheries?

The third wing of the net

Some SEF fishers say that the importance of the shelf break trawl grounds is that they form the third wing of the net.

Robison (1995) noted that virtually all mid-water foraging species share the same flight response, which is to dive into the darkness below when pursued, and retreat towards the lower end of their depth range when disturbed. It is probably this characteristic flight response that renders mid-water foraging species vulnerable to demersal trawling. Thus we visualize mid-water species foraging up through the water column each evening, 100–500 m above their normal daytime depth, before retreating back to depth as light intensities increase each morning. The gelatinous zooplankton through which these species forage phosphoresce when disturbed (Robison 1995), so the vibrating warps of a trawl approach like storms of thunder and lightning. Being extremely sensitive to vibration, the fish are herded towards their daytime depth as the trawl approaches. Where trawl grounds are shallower than their preferred maximum depth, essentially oceanic species that have foraged in over the slope during the night may unexpectedly encounter the substratum and in confusion become vulnerable to herding and trapping by the demersal trawl.

Instinctive diving and confusion after unexpected contact with the substratum was documented on videotape for orange roughy at St Patrick's Head during acoustic surveys of 1999 (Kloser and Prince, unpublished). Some roughy, startled by the video camera several metres above the bottom, swam at speed vertically into the substratum as if totally unaware of its presence. Such fish appeared dazed and disorientated as the disturbed sediment cleared around their point of impact.

This diving reflex provides an alternative explanation for the ribbon-like depth distributions of SEF species: rather than being a reflection of a lateral distribution, the ribbon-like depth distributions are lateral projections of the preferred maximum depth occupied by each species and size class. Hulley (1992) reached this conclusion to explain the down-slope zonation observed for myctophids. He considered the down-slope community structuring in species diversity, species abundances and size to be a transient phenomenon rather than a generalized zonation of the different species. Along-slope ribbon distribution patterns would be typically localized artifacts linked to hydrographic and circulatory characteristics, but produced fundamentally by the water-depth requirements of the indivdual species.

If Hulley's view is correct, the main importance of the shelf break and slope, in terms of fisheries production, is not the benthic habitat, but the fact that SEF species form aggregations along the shelf edge and can be caught in commercially viable quantities.

Mixing

In terms of primary productivity it is the topographic relief of the shelf break that is of fundamental importance to the benthopelagic species of the SEF, rather than the benthic habitat itself. The oceanic mid-water environment is characterized by its smoothness and relative homogeneity (Marshall 1979). The shelf break enhances upward mixing of SAW into the photic zone, promoting phytoplankton blooms. Primary production at the shelf break is generally an order of magnitude higher per unit of area than in adjacent waters (Young et al. 1996). This provides enhanced opportunities for feeding, which supports breeding aggregations and provides the enriched conditions critical for enhancing larval survival.

The paradox of the missing production

So what is the relative importance of primary production over the continental shelf and slope to the SEF? Crucial to this issue is the extent to which species of the SEF undertake vertical and lateral feeding movements away from the slope. If fish are primarily restricted to feeding close to the bottom, there is limited scope for gathering in the extensive but dispersed primary production of the STC. However, if key species undertake lateral and vertical migrations, primary productivity could be garnered over an extensive region of the STC.

The fishers believe that many SEF species, including orange roughy, school shark, blue grenadier, eastern gemfish, blue eye trevalla, frostfish and the warehous, forage extensively beyond the benthic environment. Many argue that species such as school shark, blue grenadier and gemfish mix with New Zealand populations of the same species. Until recently these arguments have generally been dismissed. Biologists, influenced by the main mode of fishing and research sampling (demersal trawling) together with the relative lack of large organisms in mid-water trawls, have tended to assume *a priori* a strictly demersal life style. This approach is epitomized by Koslow *et al.* (1994), who assumed that 111 of 158 species captured by demersal trawl around the slope off Tasmania were demersal, and derived biomass estimates assuming complete catchability (q = 1.0) for species such as blue grenadier, dories, whiptails, cardinal fish, oil fish, frostfish and orange roughy.

However, this suite of assumptions inevitably confronts us with the paradox of the missing production. One facet of this paradox (see above) is the mechanisms causing the observed variability of catchability of SEF species. In his discussion of orange roughy bio-energetics, Koslow (1997) approaches this paradox from a different angle. The original biomass estimates based on the area swept by randomly stratified demersal trawl prior to commercial fishing were quickly shown by declared catches, acoustic surveys and egg surveys to be an order of magnitude too low. However, primary production over the slope is an order of magnitude too small to support the biomass that existed. So where was the missing 90% of the biomass during the stratified random demersal trawl surveys? And where does the productivity that supported it come from? Koslow (1997) postulates that the missing roughy lived demersally around the seamounts and rough bottom and were invulnerable to trawl surveys. He further hypothesizes that some unknown mechanisms, such as deep-water currents, must gather and transport the missing 90% of productivity needed to sustain roughy in their slope environment. This is undoubtedly true to some extent, but probably underestimates the importance of the fish themselves in gathering dispersed oceanic productivity and transporting it back into the demersal slope environment. According to Koslow's (1997) analysis, the amount of roughy found dispersed along the slope would have been sustained by the slope's productivity. It is probable that the remaining 90% of roughy were being sustained by foraging over a broader area beyond the slope.

May and Blaber (1989) explored the middle ground using both demersal and mid-water trawls to study the fish assemblage over a small area of the shelf break off Maria I. Their approach assumed different catchabilities for each species with each net (Kenchington 1989). This approach explicitly acknowledges the broad range of SEF species, with a wide range of life styles and catchabilities, and finds the terms 'demersal' or "pelagic' to be simplistic, referring only to the extremes of a continuum. Thus, May and Blaber (1989) recorded 62 species in demersal trawls and 72 species from mid-water trawls, with 18 species being recorded with both gear types. For 10 of the 18 species caught in both gear types, May and Blaber created a category of 'dispersed' rather than calling them benthic or pelagic. In this category they placed a number of species elsewhere regarded as demersal, including blue grenadier, mirror dory, southern frostfish, eastern gemfish and spotted warehou.

The difficulty with May and Blaber's approach is that the lack of quantitative data about the catchability of SEF species leads to the use of 'guesstimates', which to some extent must recycle established assumptions. Hence, they (May and Blaber 1989) were forced to assume that school shark is a demersal species, and that many other SEF species are highly catchable with demersal trawls, e.g. feeding blue grenadier (1.17), king dory (0.95), spiky dory (0.83), eastern gemfish (0.83) and blue eye trevalla (0.83).

The risk in recycling assumptions is illustrated by the case of school shark. At times the sharks may spend periods of days to months at depths as great as 400–600 m, making extensive diurnal vertical migrations (e.g. West and Stevens 2001; Fig. 2). Moreover, a growing number of conventionally tagged individuals documented to have crossed the Tasman Sea further adds to the picture that these 'demersal' sharks may also forage extensively in mid water.

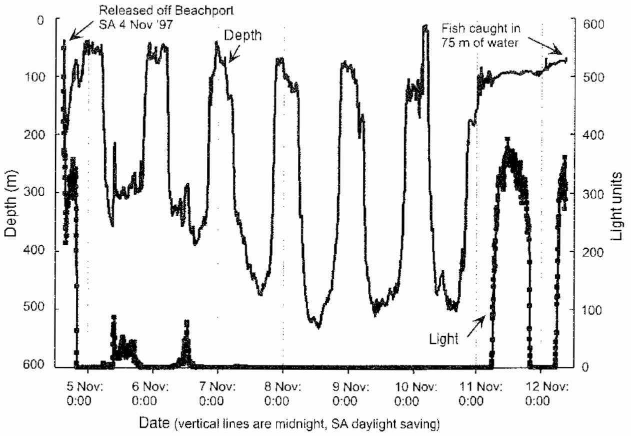


Fig. 2. Data on depth and light intensity retrieved from an archival tag carried by a school shark off South Australia, 4–12 November 1997, showing the daily vertical migrations undertaken and the low light intensity inhabited by the shark. Source West and Stevens (2001).

Given the newness of this type of technology and hence the scarcity of such studies, one wonders how many other demersal SEF species would be found to forage beyond the benthic environment if data existed. Interestingly the records of the scientific observers programme of the Australian Fisheries Management Authority (AFMA) show that – along with school shark – blue grenadier, eastern gemfish and blue eye trevalla, are regularly caught in low numbers by Japanese tuna vessels fishing over abyssal depths >100 km beyond the continental shelf (AFMA, personal communication).

Blaber and Bulman's (1987) data on the diet of selected SEF species revealed extensive vertical feeding migrations in some SEF species. Blue grenadier undertook extensive vertical migrations, feeding at night on myctophids in shallow water, but were caught demersally on the slope during the day. King dory, ocean perch and toothed whiptail were also caught in the mid water. The phenomenon of demersal-slope fish feeding on mesopelagic fauna has also been documented elsewhere (e.g. Sedberry and Musick 1978), but it is often assumed that most pelagic prey are captured near the bottom (Marshall 1979). However, 'There is a body of data to indicate that fishes hitherto considered to be bottom dwellers do make excursions well off the bottom and that these and other benthopelagic species rely to varying degrees on pelagic prey' (Marshall 1979). Macrourids, scorpaenids (Mauchline and Gordon 1984), and deep-sea squaloid sharks have all been recorded 100s to 1000s of metres above the bottom feeding on pelagic prey.

Of course, as discussed above, the movement of fish from the slope in search of mesopelagic prey can be horizontal and need not involve extensive vertical migrations (Mauchline and Gordon 1984; Blaber and Bulman 1987). Blaber and Bulman (1987) suggested that horizontal movement of predators would be negligible in their study area because the main prey species, *L. hectoris*, only occurs in large concentrations close to the shelf break, so movements away from the slope would not have brought the predatory species into contact with their prey. Although their reasoning may be correct in the context of their studies it does not exclude a different conclusion in more general terms. Their study, focussed on a restricted area of slope near Maria I. that seasonally supports large aggregations of *L. hectoris* (Young 1998), found that myctophids were extremely important to the fish they sampled. However, the narrow geographical focus of their study would have made it all but impossible to observe the diet of fish foraging on anything other than myctophids.

This point is illustrated by comparing the findings of Blaber and Bulman (1987) with those of Young *et al.* (1993). The former described the diet of jack mackerel over the slope as consisting almost entirely of myctophids, whereas the latter observed them to feed almost exclusively on krill a short distance away on the continental shelf. These results do not contradict each other but simply show an opportunistic predator switching prey to take advantage of differing prey species in different areas.

Most studies of the SEF have concentrated on relatively small areas around hotspots of primary productivity. To advance understanding of the system we must ask ourselves what these species eat when their favoured prey species are not aggregated. Hotspots in the SEF may remain inactive over broad regions for several years, so where and how do these species forage when primary production is sparse?

Young *et al.* (1997) found distinct differences in diet between southern bluefin tuna caught inshore and those caught offshore. They concluded that the migration of the tuna through south-eastern Australian shelf waters is timed to coincide with the autumn blooms of phytoplankton on the shelf. At such times the tuna feed principally on fish such as jack mackerel, pilchard *Sardinops neopilchardus* and juvenile squid *Nototodarus gouldi*, which aggregate to feed within the blooms. However, as blooms decline during winter and aggregations disperse, southern bluefin tuna move offshore to prey on alternative prey species such as gelatinous zooplankton and squid (Young *et al.* 1997).

If we accept Kashkina's (1986) conclusion that, in this region 'tunicates and coelenterates together with their associated crustaceans form the main components at the base of the food chain', the conclusion of Young *et al.* (1997) might be extended to many other SEF species besides southern bluefin tuna. Thus, we might hypothesize that, when aggregations of favoured prey species are not available along the shelf and slope, many species switch to feeding on less favoured gelatinous zooplankton communities, and to varying extents disperse to forage pelagically.

If Koslow's (1997) analysis is allowed to suggest that 90% of orange roughy productivity is derived from outside the demersal slope environment, and the density of primary production over the slope is ten times that of the adjacent STC (Young 1998), it can be hypothesized that the extended foraging grounds of orange roughy may be up to 100 times larger than the area of slope over which they are caught.

Implications for ecosytem management

Dependent on oceanic productivity rather than coastal sources, the SEF ecosystem is relatively immune to the usual external threats from eutrophication and habitat destruction facing rivers, estuaries and coastal ecosystems.

Vulnerability to targeted fishing

It has been common for some fishers to argue that because the main commercial species spend much of their life foraging outside the demersal environment they are relatively invulnerable to over exploitation with demersal fishing gear. It is true that SEF species differ in their vulnerability to overexploitation depending on the extent to which they forage in mid water. Demersal trawling will have little effect on highly pelagic oceanic species that rarely swim near trawl grounds. However, otherwise benthopelagic species such as orange roughy and gemfish, which spawn into bottom layers of water pluming up the slope, or around seamounts, have been proven to be easily over exploited. In these species the obligation to breed repeatedly makes (otherwise) long-lived adults vulnerable to fishing.

Critical habitat

Although my thesis here has been that the importance of oceanic primary production to the foraging of SEF species has previously been underestimated, this argument does not imply that preservation of benthic habitat in the SEF is unimportant. There is limited evidence that juvenile age classes of some commercial species use complex benthic habitat as refuges (Bax and Williams 2000) and this concurs with the observations and beliefs of SEF fishers. Be that as it may, protecting areas of structured benthic habitat is essential for the preservation of biodiversity in the SEF. Although in the minority, many SEF species have relatively sedentary life cycles, are truly demersal, and are dependent on undisturbed reef habitat. Long-lived demersal sharks with low fecundity are particularly vulnerable. Regrettably, the current ITQ system in the SEF has no mechanism for managing species that are not included among the 16 quota species. Biodiversity can be protected only by controlling the level of exploitation across all appropriate fisheries and by reserving sufficient non-fished areas to maintain viable populations of non-commercial obligate reef-dwelling species.

Acknowledgments

I thank the following: the fishermen of the SEF and the South East Trawl Fishing Industry Association for their generous support of this study; the Fisheries Research and Development Corporation and the Australian Fisheries Management Authorities Research Fund for funding the string of projects that has enabled this study to be undertaken; and my colleagues on the South East Fisheries Assessment Group for their data, ideas and patience.

References

Andrew, N. L., Graham, K. J., Hodgson, K. E., and Gordon, G. N. G. (1997). Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. Final Report to FRDC. Project No. 96/139.

Aron, W., and Collard, S. (1969). A study of the influence of net speed on catch. *Limnology and Oceanography* **14**, 242–9.

Bax, N., Williams, A., and Althaus, F. (1999). Development of a rapid-assessment technique to determine biological interactions of fishes, and their environment, and their role in the environment. Final Report to FRDC. Project No. 96/275. 149 pp.

Bax, N., and Williams, A. (2000). Habitat and fisheries production in the South East Fishery Ecosystem. Final Report to FRDC. Project No: 94/040.

Blaber, S. J. M., and Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345–56.

Blackburn, M. (1957). The relationship between the food of the Australian barracouta *Thyrsites attun* (Euphrasen), and recent fluctuations in the fisheries. *Australian Journal of Marine and Freshwater Research* **8**, 29–54.

Blackburn, M. (1980). Observations on the distribution of *Nyctiphanes australis* Sars (Crustacea : Euphausiidae) in Australian waters. CSIRO Australia Division of Fisheries and Oceanography Technical Paper No. 119.

Boden, B. P., and Kampa, E. M. (1967). The influence of natural light on the vertical migrations of an animal community in the sea. *Symposia of the Zoological Society of London* **19**, 15–26.

Boland, F. M. (1971). Temperature salinity anomalies at depths between 200 m and 800 m in the Tasman Sea. *Australian Journal of Marine and Freshwater Research* **22**, 55–62.

Brandt, S. B. (1981). Effects of a warm core eddy on fish distributions in the Tasman Sea off east Australia. *Marine Ecology Progress Series* **6**, 19–33.

Brooks, A. L., Brown, C. L., and Scully-Power, P. H. (1974). Net filtering efficiency of a 3-meter Isaacs–Kidd midwater trawl. *Fishery Bulletin US* **72**, 618–21.

Clark, T. A. (1973). Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fishery Bulletin US* **71**, 401–34.

Clark, T. A. (1978). Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. *Fishery Bulletin US* **76**, 495–513.

Clarke, M. R. (1966). A review of the systematics and ecology of oceanic squids. *Advances in Marine Biology* **4**, 91–300.

Clarke, M. R. (1977). Beaks, nets, and numbers. In 'The Biology of Cephalopods'. (Eds M. Nixon and J. B. Messenger.) *Symposium of Zoological Society of London* **38**, 89–126.

Cresswell, G. (1994). Nutrient enrichment of the Sydney continental shelf. *Australian Journal of Marine and Freshwater Research* **45**, 677–91.

Cresswell, G., Wells, G., and Petersen, J. (1994). Australian satellite-tracked drifters 1991–1994. Report to FRDC. CSIRO Division of Oceanography, Hobart.

Cushing, D. H. (1982). 'Climate and Fisheries.' (Academic Press: London.)

Deacon, G. E. R. (1982). Physical and biological zonation in the Southern Ocean. *Deep-Sea Research* **29**, 1–15.

Gibbs, C. F., Tomczak, M. Jr, and Longmore, A. R. (1986*a*). The nutrient regime of Bass Strait. *Australian Journal of Marine and Freshwater Research* **37**, 451–66.

Gibbs, C. F., Cowdell, R. A., and Longmore, A. R. (1986*b*). Seasonal variation of density patterns in relation to the Bass Strait cascade. *Australian Journal of Marine and Freshwater Research* **37**, 21–5.

Gibbs, C. F., Arnott, G. H., Longmore, A. R., and Marchant, J. W. (1991). Nutrient and plankton distribution near a shelf break front in the region of the Bass Strait Cascade. *Australian Journal of Marine and Freshwater Research* **42**, 201–17.

Gjøsaeter, J., and Kawaguchi, K. (1980). A review of the world resources of mesopelagic fish. FAO Technical Paper No. 193.

Godfrey, J. S., Jones, I. S. F., Maxwell, J. G. H., and Scott, B. D. (1980). On the winter cascade from Bass Strait into the Tasman Sea. *Australian Journal of Marine and Freshwater Research* **31**, 275–86.

Gordon, J. D. M, and Duncan, J. A. R. (1985). The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, Northeastern Atlantic. *Progress in Oceanography* **15**, 37–69.

Hall, M., and Quill, A. F. (1983). Biological sound scattering in an ocean eddy. *Australian Journal of Marine and Freshwater Research* **34**, 563–72.

Hallegraeff, G. M., and Jeffrey, S. W. (1993). Annually recurrent diatom bloom in spring along the New South Wales coast of Australia. *Australian Journal of Marine and Freshwater Research* **44**, 325–34.

Harbison, G. R., Biggs, D. C., and Madin, L. P. (1977). The associations of Amphipoda Hyperiidea with gelatinous zooplankton. II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep Sea Research* **24**, 465–88.

Harris, G. P., Nilsson, C., Clementson, L., and Thomas. D. (1987). The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. *Australian Journal of Marine and Freshwater Research* **38**, 569–90.

Harris, G. P., Davies, P., Nunez, M., and Meyers, G. (1988). Interannual variability in climate in Tasmania, and its effect on freshwater and marine fisheries. *Nature* **333**, 754–7.

Harris, G. P., Griffiths, F. B., Clementson, L. A., Lyne, V., and Van der Doe, H. (1991). Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. *Journal of Plankton Research* **13**, s109–s113.

Hoverkamp, S. (1989). Avoidance of nets by *Euphausia pacifica* in Dabob Bay. *Journal of Plankton Research* **11**, 907–24.

Hulley P. A. (1992). Upper-slope distributions of oceanic lanternfishes (family: Myctophidae). *Marine Biology* **114**, 365–83.

Huntley, M. E., Sykes, P. F., and Marin, V. (1989). Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata : Thaliacea) near the Antarctica in austral summer, 1983–84. *Polar Biology* **10**, 59–70.

Huyer, A., Smith, R. L., Stabeno, P. J., Church, J. A., and White, N. J. (1988). Currents off south-eastern Australia: results from the Australian Coastal Experiment. *Australian Journal of Marine and Freshwater Research* **39**, 245–88.

Hynd, J. S., and Robins, J. P. (1967). Tasmanian Tuna Survey report of first operational period. CSIRO Australia Division of Fisheries and Oceanography Technical Paper No. 22.

Johannes, R. E. (1981). 'Words of the Lagoon: fishing and marine lore in the Palau district of Micronesia.' (University of California Press: Berkeley.) 245 pp.

Johannes, R. E. (1998). The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology and Evolution* **13**, 243–6.

Kashkina, A. A. (1986). Feeding of fishes on salps (Tunicata, Thaliacea). *Journal of Ichthyology* **26**(3), 57–64.

Kenchington T. J. (1989). Estimation of catchability coefficients. *Marine Biology* **101**, 24–5.

Klaer, N. L. (2001). Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. *Marine and Freshwater Research* **52**, 399–410.

Koslow J. A. (1997). Seamounts and the ecology of deep-sea fisheries. *American Scientist* March/April, 168–76.

Koslow, J. A., Bulman, C. M., and Lyle, J. M. (1994). The mid-slope demersal fish community off southeastern Australia. *Deep Sea Research* **41**, 113–41.

Koslow, J. A., Kloser, R. J., and Williams, A. (1997). Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. *Marine Ecology Progress Series* **146**, 21–35.

Lewis, R. K. (1981). Seasonal upwelling along the south-eastern coastline of south Australia. *Australian Journal of Marine and Freshwater Research* **32**, 843–54.

Marshall, N. B. (1979). 'Developments in Deep Sea Biology.' (Blandford Press: Poole, Dorset.) 566 pp.

Mauchline, J., and Gordon, J. D. M. (1984). Ocurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **41**, 239–47.

May, J. L., and Blaber, S. J. M. (1989). Benthic and pelagic fish biomass of the upper continental slope off eastern Tasmania. *Marine Biology* **101**, 11–25.

McClatchie, S., Millar, R. B., Webster, F., Lester, P. J., Hurst, R., and Bagley, N. (1995). Bio-diversity. *Seafood New Zealand* February pp. 17–20.

Mills, C. E. (1995). Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES Journal of Marine Science* **52**, 575–81.

Newell, B. S. (1961). Hydrology of south-east Australian waters: Bass Strait and the New South Wales tuna fishing area. CSIRO Australia Division of Fisheries and Oceanography Technical Paper No. 10.

Nowara, G. B., and Walker, T. I. (1997). Effects of time of solar day, jigging method and jigging depth on catch rates and size of Gould's squid, (*Nototodarus gouldi*) (McCoy) in southeastern Australian waters. *Fisheries Research* **34**, 279–88.

Nyan Taw and Ritz, D. A. (1979). Influence of subantarctic and subtropical oceanic water on the zooplankton and hydrology of waters adjacent to the Derwent River estuary, south eastern Tasmania. *Australian Journal of Marine and Freshwater Research* **30**, 179–202.

Pagès, F., White, M. G., and Rodhouse, P. G. (1996). Abundance of gelatinous carnivores in the nekton community of the Antarctic polar frontal zone in summer 1994. *Marine Ecology Progress Series* **141,** 139–47.

Pakhomov, E. A., Perissinotto, R., and McQuaid, C. D. (1994). Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic polar fronts. *Marine Ecology Progress Series* **111**, 155–69.

Paxton, J. R. (1967). A distributional analysis for the lanternfishes (Family Myctophidae) of the San Pedro Basin, California. *Copeia* **1967(ii)**, 422–40.

Pearcy, W. G., Krygier, E. E., Mesecar, R., and Ramsey, F. (1977). Vertical distribution and migration of oceanic nekton off Oregon. *Deep Sea Research* **24**, 223–45.

Pearce, A., and Boland, F. M. (1982). Aanderaa current meter records from the New South Wales continental shelf, 1978–80. CSIRO Marine Laboratories Report No. 140.

Pearcy, W. G., Stein, D. L., and Carney, R. S. (1982). The deep-sea benthic fauna of the Northeast Pacific Ocean on Cascadia and Tufts Abyssal Plains and adjoining continental slopes. *Biological Oceanography* **1**, 375–428.

Prince, J. D. (1996). Industry survey of the 1996 eastern gemfish spawning season. FRDC Report No. 96/157. (Available from Biospherics Pty Ltd, PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D. (1999). Industry survey of the 1999 eastern gemfish spawning season. ARF Report No. 98/99–14. (Available from Biospherics Pty Ltd, PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D., Diver, G. R., and Ruiz-Avila, R. J. (1995). Socio-economic impact study of proposed closures in the eastern gemfish fishery. FRDC Report No. 95/130. (Available from Biospherics Pty Ltd, PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D., Griffin, D., and Diver G. (1997). Industry survey of the 1997 eastern gemfish spawning season. FRDC Report No. 97/147. (Available from Biospherics Pty Ltd, PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D., Griffin, D., and Diver G. (1998). Industry survey of the 1998 eastern gemfish spawning season. ARF Report No. 97/98–13. (Available from Biospherics Pty Ltd, PO Box 168, South Fremantle, WA 6162, Australia.)

Pugh, P. R. (1984). The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 7. Siphonophores. *Progress in Oceanography* **13**, 461–89.

Purcell, J. E. (1992). Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. *Marine Ecology Progress Series* **87**, 65–76.

Ridgway, K. R., and Godfrey, J. S. (1997). Seasonal cycle of the East Australian Current. *Journal of Geophysical Research* **102**, 22921–36.

Ritz, D. A., and Hosie G. W. (1982). The production of the euphausiid *Nyctiphanes australis* in Storm Bay, south east Tasmania. *Marine Biology* **68**, 103–8.

Robison, B. H. (1995). Light in the ocean's midwaters. *Scientific American* July, 49–56.

Rochford, D. J. (1972). Nutrient enrichment of eastern Australian coastal waters. I. Evans Head upwelling. CSIRO Australia Division of Fisheries and Oceanography Technical Paper No. 33.

Rochford, D. J. (1975). Nutrient enrichment of eastern Australian coastal waters. II. Laurieton upwelling. *Australian Journal of Marine and Freshwater Research* **26**, 233–43.

Rochford, D. J. (1977*a*). The present evidence for summer upwelling of north east Victoria. CSIRO Division of Fisheries and Oceanography Report No. 77.

Rochford, D. J. (1977*b*). A review of a possible upwelling situation off Port MacDonnell SA. CSIRO Division of Fisheries and Oceanography Report No. 81.

Schahinger, R. B. (1987). Structure of coastal upwelling observed off the south-east coast of South Australia during February 1983–April 1984. *Australian Journal of Marine and Freshwater Research* **38**, 439–59.

Scott, B. D. (1981). Hydrological structure and phytoplankton distribution in the region of a warm-core eddy in the Tasman Sea. *Australian Journal of Marine and Freshwater Research* **32**, 479–92.

Sedberry, G. R., and Musick, J. A. (1978). Feeding strategies of some demersal fishes of the continental slope and rise off the mid-Atlantic coast of the USA. *Marine Biology* **44**, 357–75.

Siegel, V., and Loeb, V. (1995). Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series* **123**, 45–56.

Tilzey, R. D. J. (1994). 'The South East Fishery.' (Bureau of Resource Science: Canberra.) 360 pp.

Thresher, R. E., Harris, G. P., Gunn, J. S., and Clementson, L. A. (1989). Phytoplankton production pulses and episodic settlement of a temperate marine fish. *Nature* **341**, 641–3.

Tomczak, M. (1985). The Bass Strait water cascade during winter 1981. *Continental Shelf Research* **4**, 255–78.

Tranter, D. J., Parker, R. R., and Cresswell, G. R. (1980). Are warm-core eddies unproductive? *Nature (London)* **284**, 540–2.

Tranter, D. J., Leech, G. S., and Airey, D. (1983). Edge enrichment in an ocean eddy. *Australian Journal of Marine and Freshwater Research* **34**, 665–80.

Tucker, G. H. (1951). Relation of fishes and other organisms to sound scattering of underwater sound. *Journal of Marine Research* **10**, 215–38.

West, G. J., and Stevens, J. D. (2001). Archival tagging of school shark, *Galeorhinus galeus*, in Australia: initial results. *Environmental Biology of Fishes* **60**, 283–98.

Williams, A., and Koslow, J. A. (1997). Species composition, biomass and vertical distribution of micronekton over the mid-slope region off southeastern Australia. *Marine Biology* **130**, 259–76.

Young, J. W. (1998). Ecology of midwater zooplankton and fishes off eastern Tasmania. PhD Thesis, University of Tasmania.

Young, J. W., Jordan, A. R., Bobbi, C., Johannes, R. E., Haskard, K., and Pullen, G. (1993). Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern, Tasmania, Australia. *Marine Biology* **116**, 9–18.

Young, J. W., Bradford R. W., Lamb, T. D., and Lyne, V. D. (1996). Biomass of zooplankton and micro nekton in the southern bluefin tuna fishing grounds of eastern Tasmania, Australia. *Marine Ecology Progress Series* **138**, 1–14.

Young, J. W., Lamb, T. D., Le, D., and Whitelaw, A. W. (1997). Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters of eastern, Australia. *Environmental Biology of Fishes* **50**, 275–91.

Zuev, G. V., and Nesis, K. N. (1971). 'Kal'mary i Promysel.' [Squid (Biology and Fishery). pp. 70–77, 305–39. Fisheries Research Board of Canada 1973. Translation Series No. 2598. (Deposited at Biological Station: St John's, Newfoundland.)]

Manuscript received 17 March 2000; revised 14 April and 17 November 2000, and 22 January 2001; accepted 22 January 2001

Mar. Freshwater Res., 2001, **52**, 451–62

Phytoplankton blooms and production sources on the south-east Australian continental shelf

Nicholas J. Bax[AC], *Michele Burford*[B], *Lesley Clementson*[A] *and Stevie Davenport*[A]

[A]CSIRO Marine Research, Castray Esplanade, Hobart, Tas. 7001, Australia
[B]CSIRO Marine Research, Cleveland, Qld 4163, Australia
[C]Authors listed alphabetically

Abstract. During a large-scale ecosystem study on the south-east Australian shelf in spring 1994, we opportunistically sampled a widespread phytoplankton bloom. *Thalassiosira partheneia*, a small centric diatom, was the primary species in the bloom, indicating that we had sampled the early stage of a typical short-lived spring bloom for the area. Pigment analysis indicated four distinct communities that were coincident with the regional oceanography. The bloom was strongest over the northern shelf where the East Australian Current overlaid uplifted nutrient-rich slope water, but absent at inner stations on the wide southern shelf, where slope water did not reach. The bloom was patchy over the southern outer shelf where slope water was present to the surface and local conditions were influenced by topography. Pigment and stable isotope data indicated that primary production in this area was almost entirely oceanic. A slight trend for seaward enrichment of sediment $\delta^{13}C$ is best explained by limited macroalgal growth in shallow waters. There was little fresh organic matter in the sediment even for stations under the bloom, suggesting that the bloom did not reach the seabed directly. The lack of specific zooplankton grazing pigments suggests that zooplankton grazing was minimal.

Introduction

Plankton distribution on the continental margins of the oceans is especially patchy because of the influence of physical, chemical and biological variables on *in situ* production, or because of the spatial redistribution of existing variability (Mackas *et al.* 1985). Topographic features of the shelf margins can interact with prevailing currents, producing subsurface fronts that decrease the mixed layer's depth and enhance the productivity of phytoplankton and higher trophic levels (Fournier *et al.* 1979).

Upwelling events reaching the surface have been observed annually off south-eastern Australia from January to April (Rochford 1972; Edwards 1990). Further north, these upwelling events are thought to result from the movement of the East Australian Current (EAC) eddies moving south along the east coast (Huyer *et al.* 1988) and on to the inner continental shelf (McLean-Padman and Padman 1991). Topography may have a role in enhancing upwelling in the southern part of the shelf where the three arms of the deep Bass Canyon intersect the shelf break in this area. These intersections are favoured areas for local fishers, and upwelled water has been detected regularly at the surface inshore of the largest arm of the canyon (Rochford 1972; Edwards 1990). These observations suggest that at least part of the plankton productivity in this area could derive from oceanographic features associated with the shelf-break canyons.

Two possible local sources of primary production are phytoplankton blooms, and estuarine and shallow-water vegetative production. The latter has specific importance to some juvenile fish species south-west of the study area, off the west coast of Tasmania (Thresher *et al.* 1992); however, it may not be the main production source, because terrestrial runoff and nutrients are limited. Short-lived diatom blooms occur on the continental shelf off Sydney in most years (e.g. Hallegraeff 1981) and were widespread along the entire New South Wales coastline and 700 km south to Maria Island off Tasmania, when surveyed in 1981 and 1984 (Hallegraeff and Jeffrey 1993). These authors suggested that the widespread phytoplankton blooms off south-eastern Australia contribute profoundly to fisheries production in this area (Hallegraeff and Jeffrey 1993). However, there is often a poor coupling of grazer and production dynamics in short-lived blooms, and a large fraction of the phytoplankton can be transferred directly to seabed consumers, or exported to the continental slope (Walsh *et al.* 1981).

As part of a broad ecosystem study, we studied the continental shelf between 20 and 200 m depth, bounded by Wilsons Promontory (Victoria) in the south-west and Bermagui (New South Wales) in the north-east (Fig. 1). One

10.1071/MF00001 1323-1650/01/040451

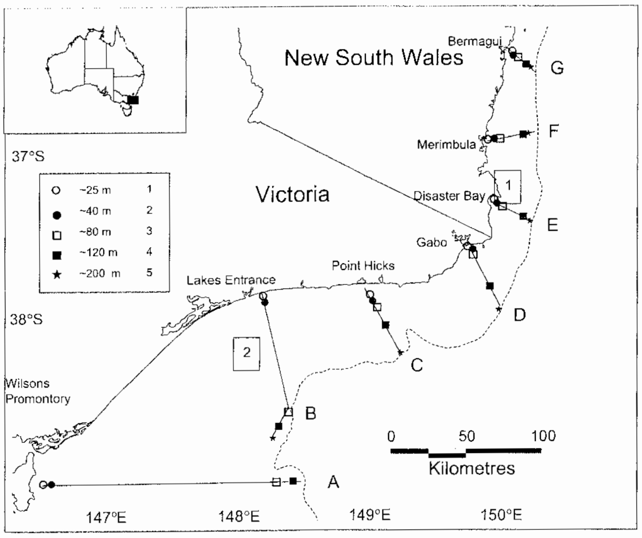


Fig. 1. The study area off south-east Australia showing the seven cross-shelf transects with five stations apiece (1, 25 m; 2, 40 m; 3, –80 m; 4, 120 m; 5, –200 m). Water-column pigments, isotopes and plankton were sampled at Stations 2 and 5. Physical oceanography, sediment pigments and isotopes were measured at all stations. Boxes 1 and 2 are the areas used to extract seasonal temperature data from SST images (see Fig. 2).

objective of this five-year study (1993–97) was to define the sources of production that sustain this ecosystem.

On the second research survey in this area — August 1994 (the austral late winter/early spring) — the clogging of the engine filters on our research vessel, the FRV *Southern Surveyor*, showed that a plankton bloom was present in the northern half of our study area. In this paper we describe the nature and extent of the phytoplankton bloom of August-September 1994, and its influence on the seabed. We describe the oceanographic conditions at the time and place of the bloom, and consider whether the widespread diatom blooms reported by Hallegraeff and Jeffrey (1993) are continuous along the south-east Australian continental shelf. By comparing water-column production with benthic processes in bloom and non-bloom areas, we go some way towards elucidating the relative roles of the different sources of primary production in maintaining system productivity on this shelf.

Methods

Sampling began on 24 August 1994 off Wilsons Promontory, on the southernmost of seven cross-shelf transects, and progressed northward to end off Bermagui on 6 September. Five stations — 25, 40, 80, 120 and 200 m water-column depth — were sampled on each transect (Fig. 1). Conductivity–temperature–depth (CTD), fluorometer, water and benthic sled samples were taken at each station. Sediments were collected by a short blade at the aft end of a rectangular opening on one of the sled skids that directed sediment into a removable stainless-steel box on the upper surface of the skid.

Physical water column properties

Water samples collected from the surface, close to the bottom, and available depths of 10, 25, 50, 75, 100 and 200 m on each CTD cast, were analysed for salinity, dissolved oxygen and nutrients (nitrates, nitrites, phosphate and silicate) by standard methods (CSIRO Marine Laboratories Report 166).

Water-mass structures at the surface and at the bottom were determined from multivariate analysis of all physical and chemical data (except nitrites, which were measured at only one depth). Because the data were approximately normally distributed, contained few zeros, and an approximately linear relationship between variables was expected, we chose Euclidean distance as an appropriate measure of dissimilarity. Hierarchical agglomerative clustering (CLUSTER) was used to form groups of samples based on between-sample similarities, and non-metric multidimensional scaling (MDS) was used to display between-sample similarities in two-dimensional space (PRIMER; Carr 1996).

NOAA-12&14 Advanced Very High Resolution Radiometer (AVHRR) data were used to generate 1-km resolution, optimally interpolated images of sea-surface temperature (Walker and Wilkin 1998). A time series of average sea-surface temperatures was computed for two boxes in the study area, chosen to represent EAC water off southern New South Wales (Box 1, Fig. 1), and cooler Bass Strait water off eastern Victoria (Box 2, Fig. 1).

Pigment analysis

Water samples for pigment analysis (4–9 L) were collected from two depths (surface and the subsurface chlorophyll maximum as determined from the fluorescence trace) at the 40 and 200 m depth stations and filtered through a 47 mm glass-fibre filter (Whatman GF/F). The pigments were extracted in acetone, filtered through a 0.2 μm membrane filter (Whatman, anatope) and analysed by HPLC. The pigments were separated as described in Wright *et al.* (1991), detected at 436 nm, and identified against standard spectra. Concentrations of chlorophyll *a*, chlorophyll *b*, β,β-carotene, and β,*e*-carotene were determined against standards (Sigma); all other pigment concentrations were determined against standards of purified pigments from algal cultures.

Multivariate analysis of pigment concentrations was used to identify regions with similar pigments and pigment concentrations. Statistical techniques were the same as those used to determine water mass structure, except the Bray–Curtis similarity index was used instead of Euclidean distance as it is more appropriate for biological quantities (Legendre and Legendre 1983). Data were transformed with natural logarithms (+1 to account for zeros) because earlier analyses had shown this transformation provided representative groupings, and a logarithmic transformation is usually appropriate for biological count data, of which these concentrations were assumed to be indicators.

Groups determined from the multivariate analyses were used as the samples in percentage similarity analyses (SIMPER) to determine the pigments contributing to within-group similarity and between-group dissimilarity (PRIMER; Carr 1996).

Phytoplankton

Intact phytoplankton specimens for taxonomic identification were taken from formalin-preserved bongo net samples (500 μm mesh, but clogged because of bloom conditions). Algal samples were examined under light and scanning electron microscopes to identify the primary phytoplankton species responsible for the dense and widespread August bloom. No attempt was made to determine phytoplankton composition with this method as the mesh size was much too large to retain anything but the most abundant (and fortunately chain forming) diatom.

Stable isotope analysis

Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) from water and sediment samples were analysed to determine the origins and fate of primary production. Water samples were obtained from 4–9 L of sample water filtered through a 47 mm glass fibre filter (Whatman GF/F). Sediment samples were obtained from a benthic sled. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per-thousand (‰) difference between the sample and conventional standards (the primary standards are Pee Dee Belemnite [a marine limestone fossil] and N_2 in air):

$$\partial X = \left[{R_{\text{sample}}}\big/{R_{\text{standard}}} - 1 \right] \times 1000$$

where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Sediment pigment analysis

Samples of 1–2 g were chipped from the frozen sediment sample. Each sample was ultra-sonicated with a Branson microtip probe for 1 min in 100% cold methanol. Extracted samples were filtered through 25-mm-diameter glass-fibre filters (Whatman GF/F) to remove particulates, diluted with deionized water in a ratio of 3:1 methanol:water, and injected into a Waters HPLC system. The spectra and HPLC retention times of the various pigments were compared with those of pigments previously isolated from standard algal cultures (Burford *et al.* 1994). Dry weights of sediment subsamples were obtained after oven-drying at 60°C for 24 h.

Results

General observations

The plankton bloom was first observed on 26 August at the deep stations off Lakes Entrance, and was present near the vessel until the survey was completed and the vessel left the study area (on 19 September). Phytoplankton clogged plankton nets at the offshore site on the Bermagui transect (phytoplankton was also present, but less abundant, at the inshore site here), at the inshore and offshore sites on the Merimbula, Disaster Bay and Gabo transects, and at the offshore site on the Lakes Entrance transect (300 km to the south of Bermagui).

Physical oceanography

Satellite images of sea-surface temperature (SST) (Plate I*a*) show cool water (12°C) in the west and hugging the inner shelf from Wilsons Promontory to beyond Lakes Entrance. There was an eddy of East Australian Current (EAC) water off Bermagui. South of this, the southern extremity of the EAC resulted in water with a surface temperature of 13–16°C. The SST time series indicates that the survey was made at the coolest part of the year, before spring warming began (Fig. 2). Annual SST images show that the EAC was receding from April to October (Bax and Williams 2000).

No ocean colour satellites covered this area at the time of the study. We had hoped to use satellite images of reflected sunlight from the available satellite to indicate the extent and duration of the bloom, but the satellite passes were in the afternoons and light levels were too low to be of use.

Multivariate analysis of *in situ* temperature, salinity and nutrients grouped stations (in statistical space and separately for surface and bottom water) with similar characteristics. Grouped stations were also contiguous in physical space, supporting the statistical groupings. There were different patterns of water-mass structure at depth and at the surface (summarized in Plate I*e* and I*f*).

Relatively cool (13.0 ± 0.9°C SD), high-nutrient (nitrates 11.7 ± 3.6 mmol L^{-1}) slope water was present at depth on all transects (e.g. Transect D, Fig. 3). This water reached only outer shelf stations on southern and middle transects (A–E), but covered the entire shelf on northern transects (F and G) (Plate I*f*). Inshore and mid-shelf stations on the southern and middle transects were vertically mixed, with very low nutrients (nitrates 1.8 ± 1.6 mmol L^{-1}) and temperatures (12.4 ± 0.9°C) suggesting that it was Bass Strait water.

At the surface, this pattern was complicated by a wedge of warmer, low-nutrient water at inshore stations on northern transects (E, F and G) that extended across the shelf on Transect D (Plate I*e*). This warmer water split the outer shelf stations into two groups: north (E, F and G) and south (A, B and C). The northern group, characterized by relatively warm (15.4 ± 1.1°C), low nutrient water (nitrates 2.0 ± 2.2 mmol L^{-1}), represents EAC water entering the study area at the north, but becoming less distinct at shallower, inshore stations where the water-column is more mixed. The southern offshore group was characterized by marginally lower temperatures (15.2 ± 0.7°C) but markedly higher nutrients (nitrates 7.6 ± 1.3 mmol L^{-1}). This may indicate greater vertical mixing of slope water in this area, although other possibilities cannot be excluded. The southern inshore group was again characterized by low nutrients (nitrates 1.8 ± 2.7 mmol L^{-1}) and lower temperatures (12.3 ± 0.9°C).

Phytoplankton

Taxonomy

Thalassiosira partheneia, a small centric diatom of 8–13 µm diameter, was identified from bongo net samples. *T. partheneia* has good food value for grazing zooplankton, although the irregular gelatinous masses it forms can be difficult for zooplankters to process (G. Hallegraeff, University of Tasmania, personal communication). No other species were identified with this highly selective gear. Analysis of pigments provided a less selective view of community composition.

Pigment analysis

Chlorophyll *a* concentrations accorded well with visual observations of bloom conditions (i.e. water colour and net clogging of bongo nets). The depth of the chlorophyll maximum was usually 25 m at offshore stations (except off Point Hicks, where it was at the surface, and Wilsons Promontory, where it was at 44 m) and 0–33 m at inshore

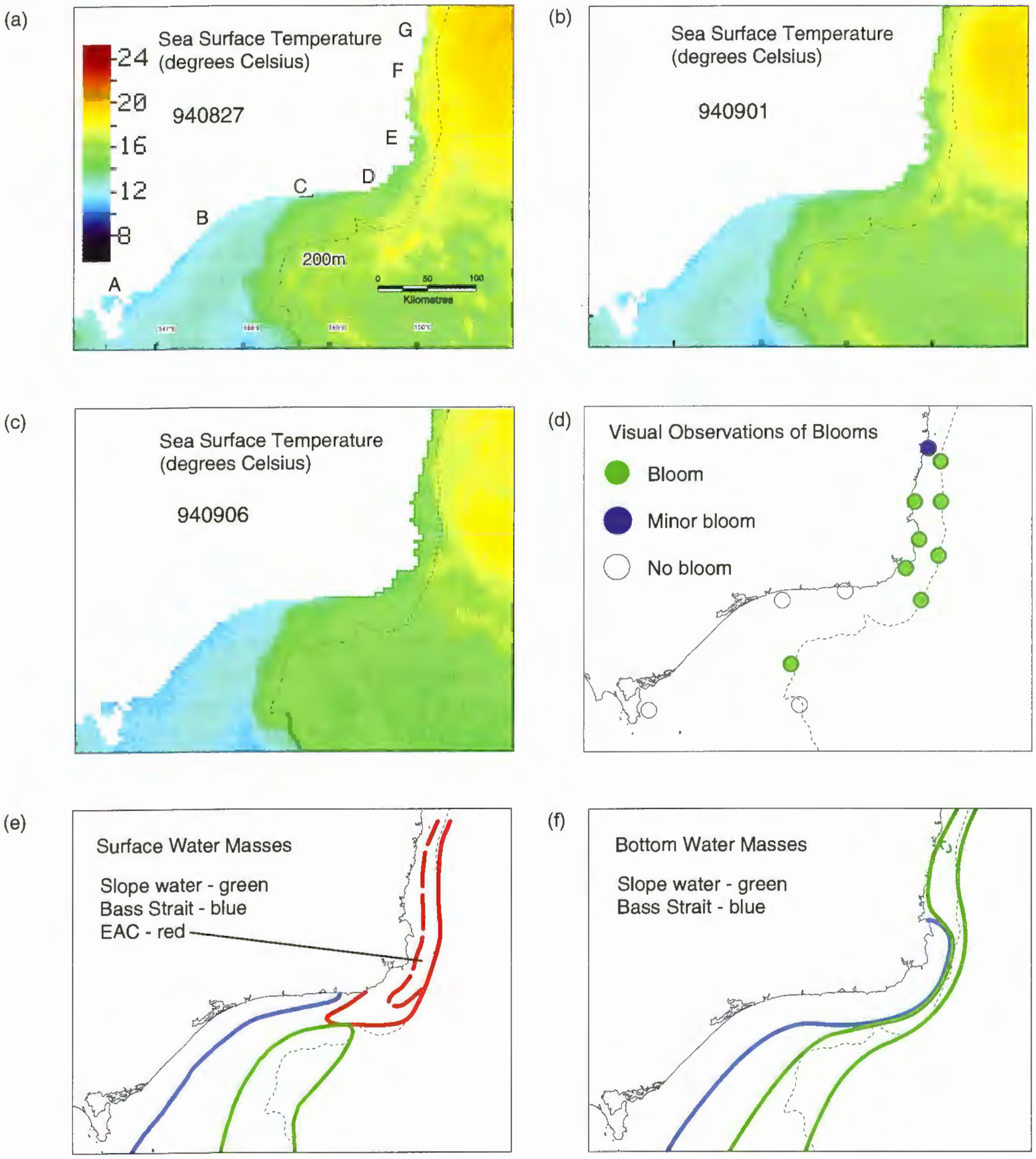


Plate I. Maps of the survey area showing *(a–c)* SST images over the course of the survey, *(d)* distribution of bloom observed from clogging of plankton nets, *(e)* water-mass at the surface, and *(f)* water-mass close to the seabed.

stations, typical depths for coastal phytoplankton blooms (Jeffrey and Hallegraeff 1989).

The mean chlorophyll concentration was 0.6 ± 0.2 µg L^{-1} (range 0.1–1.3 µg L^{-1}, $N = 28$). Chlorophyll *a* was greatest for offshore sites on the Bermagui, Disaster Bay and Gabo transects (1.65–2.20 µg L^{-1}; Table 1) and for inshore sites on the Merimbula, Disaster Bay and Gabo transects (1.07–1.76 µg L^{-1}), the densest part of the bloom. The least amounts of chlorophyll *a* coincided with the appearance of phaeophytin *a* at the northern end of the survey area (the inshore site on the Bermagui transect, 0.39 µg L^{-1}).

The most widespread pigments detected in the water-column were chlorophyll *a*, chlorophyll *b*, chlorophyll *c*, fucoxanthin, 19'-hexanoyloxyfucoxanthin, diadinoxanthin and β,β-carotene, indicating a phytoplankton community dominated by diatoms and prymnesiophytes. Chlorophyllide *a* was detected at all stations except the inshore sites on the Point Hicks, Lakes Entrance and Wilsons Promontory transects. This probably indicates the presence of senescent diatoms.

Other widespread pigments were: 19′-hexanoyloxyfucoxanthin, a major carotenoid of

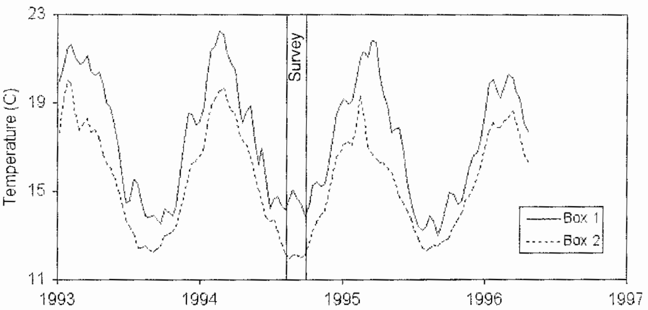


Fig. 2. Average sea-surface temperature estimated from SST images off the NSW (Box 1) and Victorian (Box 2) coast. See Fig. 1 for locations of boxes.

prymnesiophytes (coccolithophorids); alloxanthin, an indicator for cryptomonads; and chlorophyll *b*.

Several pigments were found only on southern transects, especially on inshore stations. Prasinoxanthin, an indicator for some prasinophytes (Wright *et al.* 1991; Millie *et al.* 1993), was identified from Wilsons Promontory to Gabo Island, but not at Lakes Entrance; zeaxanthin, an indicator of prokaryotic cyanobacteria (Thiel *et al.* 1988/1989), was found on all transects from Wilsons Promontory to Gabo Island. Conversely, a peak in the chromatograms suggestive of chlorophyllide *a* or a chlorophyll *a* derivative was present at all stations except the inshore sites on the Point Hicks, Lakes Entrance and Wilsons Promontory transects.

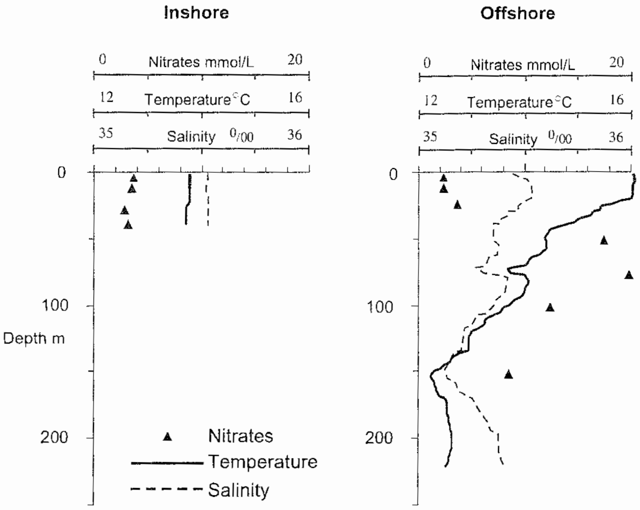


Fig. 3. Temperature, salinity and nutrient (nitrates) profiles with depth for the inshore and offshore site on Transect D (Gabo Island).

Violaxanthin, a pigment of prasinophytes and chlorophytes, was found only at inshore Point Hicks.

The grazing indicator pigments, astaxanthin and phaeophorbide, were not detected.

Algal communities

The stations could be grouped into four on the basis of their pigment concentrations; the largest of these groups could be further subdivided into a northern and southern group (Fig. 4 and Plate II*b*).

Table 1. Combined concentrations of pigments at the surface and at the depth of the chlorophyll maximum (Cmax) on the south-east Australian continental shelf in August and September 1994

(See Table 2 for full pigment names)

Transect	Water depth(m)		Pigment concentrations (ng L^{-1})														
			Chlorophyll														
	Station	Cmax	*c*3	*c*1+*c*2	*a*	*b*	19'-but	Fucox	19'-hex	cis-fuc	Prasin	Viola	Diadino	Allox	Zeax	Phytin *a*	β,β-car
Bermagui	46	33	0	141	390	55	0	140	79	0	0		51	15	0	246	0
	201	25	1,093	1,544	1,728	0	0	1,308	277	234	0		216	0	0	0	75
Merimbula	45	22	411	668	1,065	0	0	661	104	87	0		139	0	0	0	85
	152	29	454	680	835	89	0	460	213	100	0		146	0	0	0	31
Disaster Bay	44	25	573	662	1,763	0	0	847	51	147	0		155	27	0	0	92
	245	25	979	1,372	2,196	120	0	1,350	311	254	0		267	67	0	0	100
Gabo Island	43	25	463	644	1,567	251	0	790	133	193	111		174	66	32	0	97
	225	20	1,055	1,220	1,650	56	0	1,247	182	213	0		210	29	0	0	77
Point Hicks	42	15	0	117	846	260	0	36	87	0	67	*	25	32	71	0	48
	236	25	317	435	1,373	223	0	332	198	90	54		78	54	33	0	56
Lakes Entrance	42	27	0	81	549	149	0	0	54	0	0		0	0	66	0	0
	210	25	248	438	1,367	222	0	409	172	0	0		103	71	15	0	55
Wilsons Prom.	45	18	0	221	1,363	328	0	145	193	0	0		68	85	41	0	62
	200	44	195	308	668	127	29	295	127	0	25		56	24	0	0	19

*, presence of violaxanthin.

Northern and southern offshore group (1 and 1b). This was the largest group with 10 of the 14 stations. It generally had greater pigment concentrations than the remaining stations, especially chlorophyll *a*, chlorophyll *c*3, chlorophyll *c*1+*c*2, fucoxanthin, and diadinoxanthin (Table 2). This indicates greater abundance of Prymnesiophyceae, as all groups had moderate concentrations of 19'-hexanoyloxyfucoxanthin, although chlorophyll *c*3 can also indicate diatoms (12% of 73 strains of diatoms tested had *c*3 instead of *c*1; Jeffrey *et al.* 1997).

The northern subgroup was distinguished from the southern offshore group by the absence of prasinoxanthin (lack of Prasinophyceae), and 19'-butanoyloxyfucoxanthin and zeaxanthin.

Southern inshore group (2). This group lacked chlorophyll *c*3, and 19'-butanoyloxyfucoxanthin, but had 19'-hexanoyloxyfucoxanthin, which suggests that Prymnesiophyceae were absent (Table 2). The presence of prasinoxanthin indicated the presence of Prasinophyceae.

Lakes Entrance inshore station (3). This station was the most dissimilar from all other stations. Many pigments were absent, indicating a lack of (at least) Prymnesiophyceae, Prasinophyceae and Cryptophyta. Other pigments were present only at low levels.

Bermagui inshore station. This station has much in common with the southern inshore stations, but lacked Prasinophyceae. It was distinguished from all other groups by the presence of phaeophytin *a*, a breakdown product of chlorophyll *a*.

Stable isotope analysis

The mean $\delta^{13}C$ value for POM in the water-column was –21.0 ± 1.6‰ (range –24.9 to –18.7‰, $N = 28$). Whole phytoplankton had a similar mean $\delta^{13}C$ value of –20.5 ± 0.9‰. There was no difference in $\delta^{13}C$ values between inshore and offshore stations or between transects (two-way ANOVA on transects and stations, $N = 28$, $P > 0.25$ in both cases), and no difference between stations in and away from the bloom (*t*-test, $N = 28$, $P = 0.86$).

The mean $\delta^{15}N$ value for water-column POM was 7.1 ± 3.9‰ (range 2.3–18.2‰, $N = 28$), similar to the average $\delta^{15}N$ of whole phytoplankton (6.2 ± 2.3‰, $N = 4$). There were no significant differences in $\delta^{15}N$ values in water-column particulates between transects, although there were between inshore and offshore stations (two-way ANOVA on transect and station, $P = 0.195$ and 0.005, respectively). This was due to enrichment at inshore stations on southern transects (Wilsons Promontory, Lakes Entrance and Point Hicks; two-way interaction, $P = 0.037$).

Overall, $\delta^{13}C$ and $\delta^{15}N$ values were similar at the surface and at the subsurface chlorophyll maximum depth (paired *t*-test, $N = 14$, $P > 0.50$ and $P > 0.40$, respectively). However, on the southern inshore transects where $\delta^{15}N$ enrichment was detected, subsurface (25–27 m) $\delta^{13}C$ was 4–5‰ greater than at the surface, whereas subsurface $\delta^{15}N$ was 5–10‰ less.

Sediments

Pigment analysis

Most sediment samples (36 of 50) contained chlorophyll *a* and phaeophorbide *a* and/or phaeophorbide-like pigments. Only six sediment samples contained chlorophyll *a* and no phaeophorbides; eight samples contained neither chlorophyll *a* nor phaeophorbides. In all samples where both chlorophyll *a* and phaeophorbides were present, the concentration of phaeophorbides was much greater than that of chlorophyll *a* (by 5.6 to >400 times). Other pigments may have been present but masked by phaeophorbides.

Chlorophyll a. Chlorophyll *a* is present in undegraded phytoplankton cells (Thiel *et al.* 1988/1989) and benthic algae (Burford *et al.* 1994). It was found in sediments at all sites, except those in depths greater than 185 m, and at the 85 m site on the Lakes Entrance transect (Plate II*a*). The mean value of chlorophyll *a* in the sediments was 0.27 ± 0.23 $\mu g\ g^{-1}$ (range 0.00–0.84 $\mu g\ g^{-1}$, $N = 46$).

Chlorophyll *a* in the sediment generally decreased with increasing water depth ($r = -0.49$, $P = 0.0008$, $N = 43$; Plate II*a*). There was no significant relationship between chlorophyll *a* concentrations in the sediment and those in the water-column.

Phaeophorbides. Phaeophorbides are chlorophyll degradation products and indicate the presence of faecal pellets from metazoan and/or macrobenthos grazing on phytoplankton (Thiel *et al.* 1988/1989).

Phaeophorbides (phaeophorbide *a* and phaeophorbide *a*-like pigments) were detected in sediments from most sites (except the deepest) on all northern transects (D–G) but only at shallow sites (<59 m) on the southern transects (A–C). Where phaeophorbides were present in the sediment, they were abundant (mean 9.5 $\mu g\ g^{-1}$; range 0–66.1 $\mu g\ g^{-1}$).

Phaeophorbide concentrations were correlated with sediment chlorophyll *a* concentrations ($r = 0.29$, $P = 0.05$; $N = 46$) and, like chlorophyll *a*, negatively correlated with depth ($r = -0.31$, $P = 0.08$; $N = 33$). However, the negative correlation with depth was not strong; greatest concentrations occurred somewhere between the shallowest station and the mid-shelf station on many transects. No phaeophorbides were found at the outer edge of the continental shelf.

Stable isotope analysis

Mean sediment $\delta^{13}C$ was –21.9 (± 0.9‰,), close to that for POM in the overlying water-column (–21.0 ± 0.9‰) and whole phytoplankton collected from the bloom (–20.5 ± 0.9 ‰). Most transects showed a trend for a seaward enrichment in $\delta^{13}C$ values ($r = 0.652$, $P < 0.001$; $N = 33$).

Mean sediment $\delta^{15}N$ was 7.0 (± 0.8‰), close to water-column POM values (7.1 ± 3.9‰) and whole phytoplankton

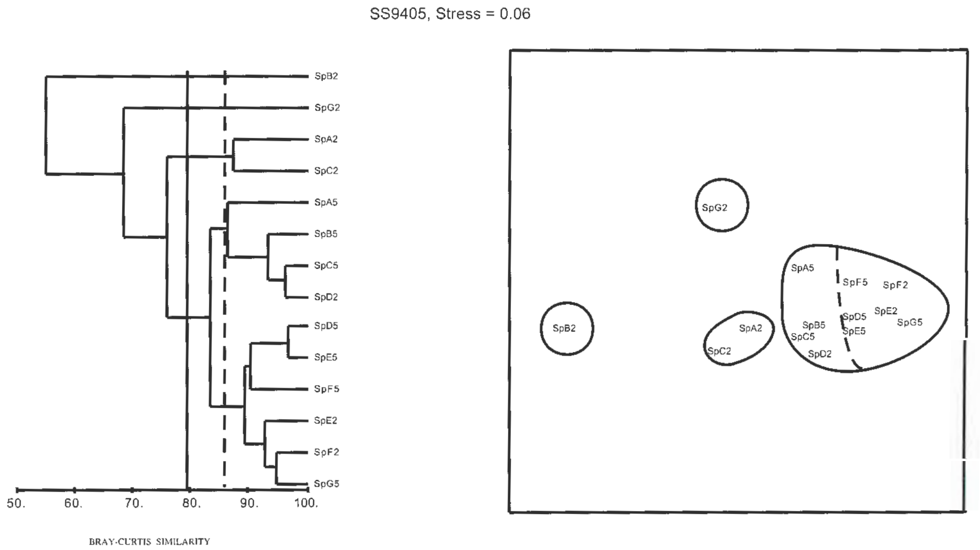


Fig. 4. Cluster analysis and MDS of pigment concentrations for combined water samples from the surface and chlorophyll maiximum at the inshore (2) and offshore (5) station on the seven (A–G) cross-shelf transects.

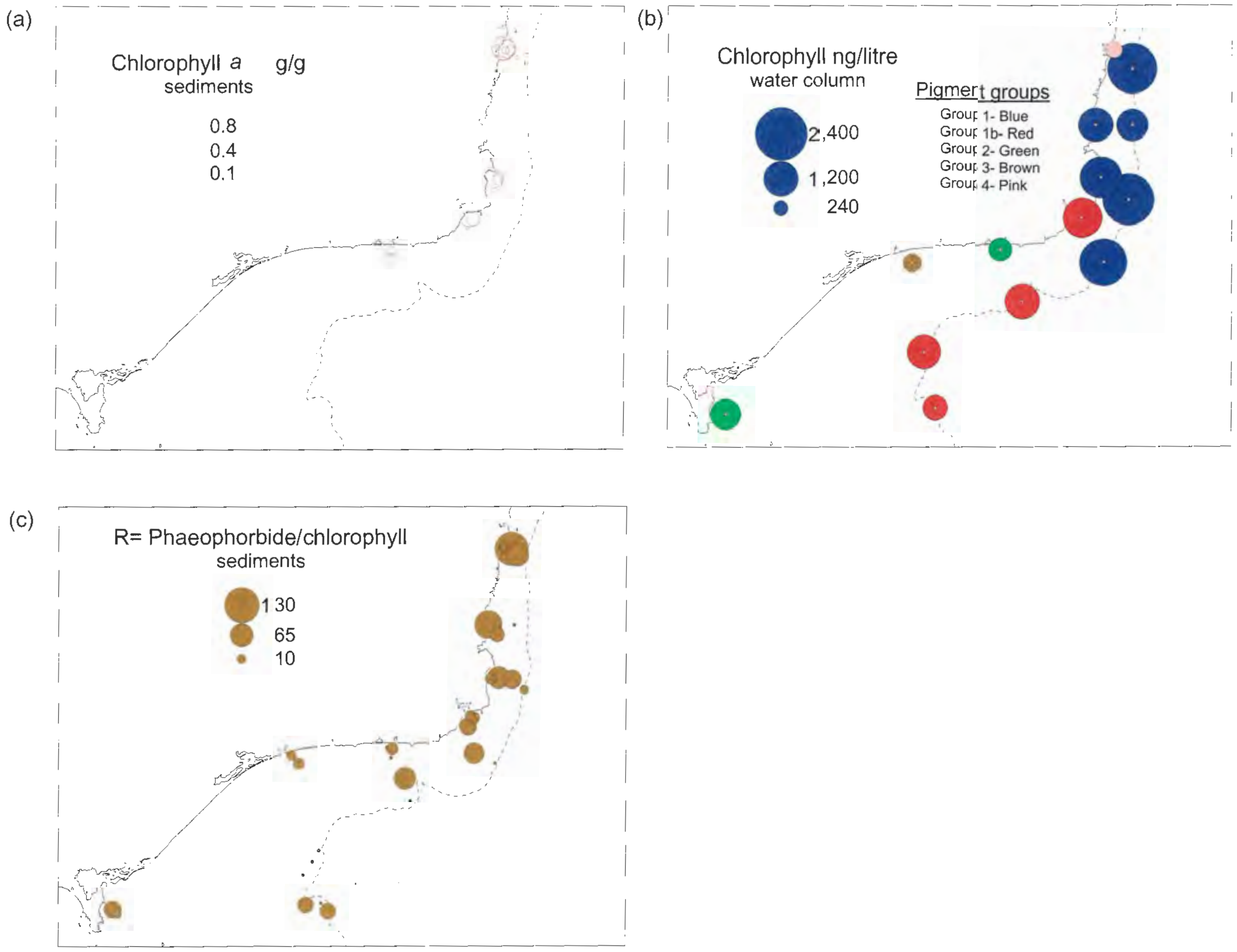


Plate II. Maps of the survey area showing *(a)* sediment chlorophyll *a* concentrations, *(b)* water-column pigment groups and chlorophyll *a* concentrations and *(c)* the ratio of sediment phaeophorbides to chlorophyll *a*.

Table 2. Average concentration (ng L^{-1}) of pigments at groups of stations selected in multivariate analyses

Bold numbers represent pigment concentrations that accounted for 50% of the dissimilarity between that group and others in the comparison

	North	South offshore	South inshore	Lakes Entrance inshore	Bermagui inshore
Cluster group:	1a	1b	2	3	4
Status of bloom:	Bloom		Non-bloom		End-bloom
Chl *c*3	**761**	**305**	**0**	**0**	**0**
Chl *c*1 + *c*2	1,024	456	169	81	141
Peridinin	0	0	0	0	0
19'-but-fucoxanthin	0	7	0	0	0
19'-hex-fucoxanthin	190	157	140	54	79
Fucoxanthin	**1,152**	527	**91**	**0**	140
Prasinoxanthin	0	**47**	**33**	0	0
Diadinoxanthin	189	103	47	**0**	51
Alloxanthin	20	54	58	0	15
Diatoxanthin	69	0	0	0	0
Lutein	0	0	0	0	0
Zeaxanthin	**0**	**20**	**56**	66	0
Chl *a*	1,539	1,244	1,104	549	390
Chl *b*	**44**	**206**	294	149	55
Phaeophytin *a*	0	0	0	0	**246**
Phaeophytin *b*	0	0	0	0	0
Pyrophytin *b*	0	0	0	0	0
β,e-carotene	0	0	0	0	0
β,β-carotene	77	57	55	**0**	**0**
Violaxanthin	0	0	1	0	0
Number in group	6	4	2	1	1

collected from the bloom (6.19 ± 2.5‰) with significant seaward enrichment ($r = 0.721$, $P < 0.001$; $N = 33$). Greatest values were at the southern inshore stations.

Discussion

The phytoplankton bloom detected in late winter 1994 was extensive, stretching 300 km from the southern limit to the end of sampling in the north. It crossed the entire shelf (40 km) in the northern part of the study area, but further south, where the shelf is broader (up to 150 km), the bloom became patchy and was restricted to the outer shelf. The bloom had much in common with earlier descriptions of spring blooms off south-east Australia, occurring at the same time of the year, and resulting from increased biomass of a particular diatom species, *Thalassiosira partheneia* (Dakin and Colefax 1940; Hallegraeff and Jeffrey 1993).

Spring phytoplankton blooms off south-east Australia

Spring phytoplankton blooms on the south-east Australian continental shelf were first studied in the 1930s (Dakin and Colefax 1940). Subsequent researchers showed that the phytoplankton blooms (indicated by chlorophyll peaks over the continental shelf and slope) off south-east Australia were irregular and short-lived (reviewed by Hallegraeff and Jeffrey 1993). Blooms resulted from East Australian Current (EAC)-mediated intrusion of nutrient-rich slope water on to the continental shelf, possibly enhanced by northerly winds (Tranter *et al.* 1982, 1986; Huyer *et al.* 1988; Cresswell 1994).

The time series of sea-surface temperatures indicated that our survey occurred before warming of the surface water had begun; the EAC was in retreat. Relatively cool, low salinity, high nutrient slope water was present at depth on all outer stations. *Thalassiosira partheneia*, a diatom that typically appears at the start of the annual spring bloom off NSW, dominated this bloom, suggesting that we encountered early bloom conditions (Jeffrey *et al.* 1982; Hallegraeff and Jeffrey 1993). In addition to chlorophyll *a*, the most widespread pigments in the water-column on this survey were chlorophyll *c*, β,β-carotene, fucoxanthin and diadinoxanthin — pigments indicative of diatom communities (Jeffrey *et al.* 1997). The absence of peridinin, indicative of dinoflagellates that typically follow diatoms in bloom development in this area (Hallegraeff and Jeffrey 1993), reinforces the conclusion of early bloom conditions.

In contrast to the features suggesting early bloom conditions, the presence of phaeophytin *a* at the inshore northern station (at 0.2 µg L^{-1} it was twice chlorophyll *a* levels of 0.1 µg L^{-1}) indicates algal breakdown products associated with mortality and/or grazing. Phaeophytin *a* was not detected at any other station. This suggests that the bloom was coming to an end in the north of the survey area. Although water-column chlorophyll and other pigment levels at the inshore northern station were the least of any stations sampled, sediment pigment concentrations were among the greatest, suggesting that the bloom here may have been as large as elsewhere in the study area, but short-lived or had started earlier. Blooms in this area are typically short-lived; the spring bloom is the most regular, occurring in August–September but lasting a month and sometimes less (Hallegraeff and Jeffrey 1993).

The dominant algal community in the study area, as determined by water-column pigments (Plate II*b*), extended across the northern shelf but was restricted to offshore waters on the southern shelf. Southern offshore stations differed from the northern stations (forming a subgroup in the analyses) by generally having lower overall pigment levels but also having prasinoxanthin, zeaxanthin and greater chlorophyll *b* concentrations, pigments also associated with southern inshore sites and indicating Prasinophyceae. Bloom conditions were only observed at some of the southern offshore stations, suggesting that either the bloom was only starting in this area or that the bloom may be patchy at these southern stations.

The distributions of the algal communities determined from pigments (Plate II*b*) matched the distribution of surface water masses in the area (Plate I*e*), suggesting a link between oceanography and the extent of the bloom. Phytoplankton blooms require sufficient nutrients and a stable (or stratified) upper water-column at least to the depth of the photic zone, where phytoplankton have optimum light conditions to photosynthesize and grow. Nutrients are generally low on the shelf in this area except where nutrient-rich subantarctic water flows onto the outer shelf. Subantarctic water was evident at depth on all outer shelf stations and extended to inshore stations in the north where the continental shelf is narrower (Plate I*f*); subantarctic water at depth was generally associated with stations where a bloom was observed or may have been imminent. Stations where a bloom was observed (with the exception of the Lakes Entrance offshore station) were also overlain by warmer, saltier, but nutrient-poor, EAC water; the overlying EAC water provided the stable upper water-column necessary for bloom conditions. We conclude that the extensive bloom on the northern shelf resulted from the influence of the EAC eddies leading to upper water-column stability and Ekman-forced uplifting of nutrient-rich subantarctic water. The stabilizing effect of EAC water was lacking at southern offshore stations and uplifting of nutrient-rich subantarctic water reached the surface. Uplifting is a patchy phenomenon caused by the incidence of current on local topography. The bloom was also patchy, and we suggest that its extent is influenced by local topography at these southern stations. There were no blooms at inshore southern stations, where there was no nutrient-rich subantarctic water.

Earlier researchers on the phytoplankton blooms in this area concluded that diatom blooms were both large (greatest values of chlorophyll reported for Australian coastal waters at time of their publication) and widespread, extending along the entire New South Wales coastline and continuing down to Maria Island, off Tasmania (Hallegraeff and Jeffrey 1993). However, the surveys on which their results were based did not cover the area between Eden and Maria Island (over 600 km linear distance), or the eastern Victorian and northern Tasmanian continental shelves, coincidentally much of the area of our ecosystem study. This is also the area where the continental shelf is broadest, and the inner shelf is bathed in nutrient-poor Bass Strait water. As shown in this study, diatom blooms may not extend to this inner shelf. In the absence of EAC water, blooms on the outer shelf may also be expected to be patchy.

Origins of primary production in this area

One of our aims in this study was to determine the origin(s) of the primary production that provides energy to this shelf ecosystem; pelagic plankton blooms are only one of the possible sources of primary production on a shelf ecosystem. However, the $\delta^{13}C$ values of water-column particulates and sediments in this study (–21.0 ± 1.6‰ and –21.9 ± 0.9‰, respectively) are typical of the temperate marine phytoplankton: –24 to –18‰ (Fry and Sherr 1984), –25.3 to –19.8‰ (Rau *et al.* 1990), –22‰ (Boutton 1991), suggesting little or no terrestrial input. There was no relationship between POM $\delta^{13}C$ values and depth, in contrast to other areas where terrestrial sources were shown to contribute to primary production in nearshore areas (Fontugne and Jouanneau 1987; Thornton and McManus 1994; Riera and Richard 1996). However, sediment $\delta^{13}C$ was slightly enriched with depth, suggesting at least some terrestrial input (e.g. Hedges and Parker 1976; Shultz and Calder 1976).

This slight seaward enrichment in sediments could indicate minor terrestrial input; however, the absence of chlorophyll *b* indicates that macrophytes are not important contributors to the sediment (Cariou-Le Gall and Blanchard 1995), and the absence of lutein and phaeopigments *b* suggests that there is insignificant input of terrestrial plant detritus (Abele-Oeschger 1991). The trend for seaward enrichment of sediment $\delta^{13}C$ may result from limited macroalgal growth in shallow waters.

Benthic productivity

We have shown that the origin of production in this area is almost entirely marine phytoplankton. In this section, we examine whether the phytoplankton bloom contributes directly to benthic productivity.

We found far fewer pigments in the sediments than in the upper water-column, primarily chlorophyll *a* and phaeophorbides. The greatest values of chlorophyll *a* in the sediments, indicative of benthic algae and settling of phytoplankton and faecal pellets from the water-column, were at depths of 30–80 m. Chlorophyll *a* concentrations decreased at greater depths and it was absent from the deepest sites on each transect. Sediment chlorophyll *a* concentrations depend on the productivity of the overlying water-column, and the system through which it must pass to reach the seafloor, typically declining with increased depth (e.g. Grebmeier *et al.* 1988), unless grazing pressure is very low (Thiel *et al.* 1988/1989).

The chlorophyll degradation products in sediment samples from the south-east Australian shelf were almost entirely phaeophorbides. The high ratio of phaeophorbides to chlorophyll *a* in sediments where both pigments were present (mean $R = 13.2$; range 5.6–402.6) indicates that the phytodetritus in the sediment is highly degraded with little input of fresh phytoplankton. Phaeophorbides are breakdown products of chlorophyll through metazoan grazing and are the major form of degraded chlorophyll found in faecal pellets (Patterson and Parsons 1963; Lorenzen 1967). The lack of phaeophorbides at the depths of the shelf break indicates that rapid grazing of the phytoplankton bloom was not the reason that chlorophyll *a* failed to reach the seabed. This is supported by the lack of grazing indicator pigments, astaxanthin and phaeophorbide, in water-column samples. This suggests that there was little water-column grazing of the early spring diatom bloom in this area.

There was little relation between water column chlorophyll and sediment chlorophyll *a* or phaeophorbides in this study. The lack of a relationship may be due to the relatively long half life of chlorophyll *a* in the sediments (13–25 days in sediments devoid of macrofauna) (Grebmeier *et al.* 1988; Josefson and Conley 1997) or because primary production gets transported into the area from upcurrent locales (Boon *et al.* 1998). In this area, where EAC-driven currents along the outer shelf and slope may be 30 cm s^{-1} or more, production reaching the sediment may have originated more than 500 km upstream. This can lead to local enriched zones (Josefson and Conley 1997). The areas of fine sediments at the head of branches of the Bass Canyon and video observations showing marine snow moving up over the lip of the shelf, suggest that oceanographic uplifting along the shelf break provides nutrients and other potential food from slope waters. This has led to the development of productive fishing areas at the shelf break (Bax and Williams 2001).

Conclusions

The phytoplankton bloom encountered in spring 1994 was typical of spring blooms along this coast. The dominant diatom species in the bloom and the chlorophyll *a* concentrations indicated early spring bloom conditions.

The bloom occurred in the stratified waters to the north, where warmer EAC waters overlayed cooler shelf water, and was starting along the shelf break in the south where there was uplifting of high nutrient slope water.

Phaeophorbides present at the northern inshore station indicate phytoplankton breakdown, suggesting that the spring 1994 bloom was to be short-lived.

Pigments detected in the water-column and sediments indicate an oceanic phytoplankton source for this area. However, sediment organic matter was highly degraded with little fresh chlorophyll, indicating that the phytoplankton bloom did not contribute directly to sediment organic matter.

Topographic features enhancing oceanic uplifting may provide nutrient input at the shelf break, leading to important fishing areas.

Acknowledgments

It is a pleasure to thank our many colleagues who contributed to this study. Electron microscopy of the blooming algae was conducted by Dr Tony Rees and Gary Critchley, and Dr Gustaaf Hallegraeff identified the algae from these images. Chris Rathbone provided the SST images, and Dr David Griffin provided the seasonal temperature analyses. Dr Stuart Bunn and Ms Sue Leighton analysed the isotope samples, and Josh Mylne analysed the sediment pigments. High school students gained their first experience of research work in separating plankton samples. Mr Bruce Barker developed the maps and figures. Ms Toni Cracknell assisted with word processing. The study would not have occurred without the Captain and crew of FRV *Southern Surveyor*. The research was supported by Grant 94/040 from the Fisheries Research and Development Corporation. Earlier versions of the paper benefited from reviews by Drs David Griffin, Jock Young and David Millie.

References

Abele-Oeschger, D. (1991). Potential of some carotenoids in two recent sediments of Kiel Bight as biogenic indicators of phytodetritus. *Marine Ecology Progress Series* **70**, 83–92.

Bax, N. J., and Williams, A. (Eds) (2000). Habitat and fisheries productivity in the South East Fishery. Final report to FRDC Project 94/040, (CSIRO Marine Research, Hobart, Tasmania, Australia.) 495 pp.

Bax, N. J., and Williams, A. (2001). Seabed habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring. *Marine and Freshwater Research* **52**, 491–512.

Boon, A. R., Duineveld, G. C. A., Berghuis, E. M., and van der Weele, J. A. (1998). Relationships between benthic activity and the annual phytopigment cycle in near-bottom water and sediments in the southern North Sea. *Estuarine, Coastal and Shelf Science* **46**, 1–13.

Boutton, T. W. (1991). Stable carbon isotope ratios of natural materials: II. Atmospheric, terrestrial, marine, and freshwater environments. In 'Carbon Isotope Techniques'. (Ed. D. C. Coleman and B. Fry.) (Academic Press.)

Burford, M. A., Long, B. C., and Rothlisberg, P. C. (1994). Sedimentary pigments and organic carbon in relation to microalgal and benthic faunal abundance in the Gulf of Carpentaria. *Marine Ecology Progress Series* **103**, 111–17.

Cariou-Le Gall, V., and Blanchard, G. F. (1995). Monthly HPLC measurements of pigment concentration from an intertidal muddy sediment of Marennes-Oléron Bay, France. *Marine Ecology Progress Series* **121**, 171–9.

Carr, M. R. (1996). 'PRIMER User Manual; Plymouth Routines in Multivariate Ecological Research.' (Plymouth Marine Laboratory: England.)

Cresswell, G. (1994). Nutrient enrichment of the Sydney continental shelf. *Australian Journal of Marine and Freshwater Research* **45**, 677–91.

Dakin, W. J., and Colefax, A. N. (1940). The plankton of the Australian coastal waters off New South Wales. University of Sydney, Department of Zoology, Monograph No. 1.

Edwards, R. J. (1990). Upwelling could hold clues to fish patterns. *Australian Fisheries* **49**, 18–20.

Fontugne, M. R., and Jouanneau, J. M. (1987). Modulation of the particulate organic carbon flux to the ocean by a macrotidal estuary: evidence from measurements of carbon isotopes in organic matter from the Gironde system. *Estuarine, Coastal and Shelf Science* **24**, 377–87.

Fournier, R. O., van Det, M., Wilson, J. S., and Hargreaves, N. B. (1979). Influence of the shelf-break front off Nova Scotia on phytoplanktion standing stock in winter. *Journal Fisheries Research Board Canada* **36**, 1228–37.

Fry, B., and Sherr. E. B. (1984). δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* **27**, 13–47.

Grebmeier, J. M., McRoy, C. P., and Feder, H. M. (1988). Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. *Marine Ecology Progress Series* **48**, 57–67.

Hallegraeff, G. M. (1981). Seasonal study of the phytoplankton pigments and species at a coastal station off Sydney: importance of diatoms and the nanoplankton. *Marine Biology* **61**, 430–40.

Hallegraeff, G. M., and Jeffrey, S. W. (1993). Annually recurrent diatom blooms in spring along the New South Wales coast of Australia. *Australian Journal of Marine and Freshwater Research* **44**, 325–34.

Hedges, J. I., and Parker, P. L. (1976) Land-derived organic matter in surface sediments from the Gulf of Mexico. *Geochimica et Cosmochimica Acta* **40**, 1019–29.

Huyer, A., Smith, R. L., Stabeno, P. J., Church, J. A., and White, N. J. (1988). Currents off south-eastern Australia: results from the Australian Coastal Experiment. *Australian Journal of Marine and Freshwater Research* **39**, 245–88.

Jeffrey, S. W., and Hallegraeff, G . M. (1989). Phytoplankton ecology of Australasian waters. In 'Biology of Marine Plants'. (Eds M. Clayton and R. King.) (Longman and Cheshire: Melbourne.)

Jeffrey, S. W., Hallegraeff, G. M., and Heron, A. C. (1982). Phytoplankton, marine food chains and their relation to ocean dynamics. CSIRO Marine Laboratories Research Report 1979–1981.

Jeffrey, S. W., Llewellyn, C. A., Barlow, R. G., and Mantoura, R. F. C. (1997). Pigment processes in the sea: a selected bibliography. In 'Phytoplankton Pigments in Oceanography: Guidelines to Modern Methods'. (Eds S. W. Jeffrey, R. F. C. Mantoura and S. W. Wright.) pp. 167–78. (UNESCO: Paris.)

Josefson, A. B., and Conley. D. J. (1997). Benthic response to a pelagic front. *Marine Ecology Progress Series* **147**, 49–62.

Legendre, L., and Legendre, P. (1983). 'Numerical Ecology.' (Elsevier: New York.)

Lorenzen, C. J. (1967). Vertical distribution of chlorophyll and phaeopigments: Baja California. *Deep-Sea Research* **14**, 735–45.

Mackas, D. L., Denman, K. L., and Abbott, M. R. (1985). Plankton patchiness: biology in the physical vernacular. *Bulletin of Marine Science* **37**, 652–74.

McLean-Padman, J., and Padman, L. (1991). Summer upwelling on the Sydney inner continental shelf: the relative roles of local wind forcing and mesoscale eddy encroachment. *Continental Shelf Research* **11**, 321.

Millie, D. F., Paerl, H. W., and Hurley, J. P. (1993). Microalgal pigment assessments using high performance liquid chromatography: a synopsis of organismal and ecological applications. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2513–27.

Patterson, J., and Parsons, T. R. (1963). Distribution of chlorophyll *a* and degradation products in various marine materials. *Limnology and Oceanography* **8**, 355–6.

Rau, G. H., Teyssie, J.-L., Rassoulzadegan, F., and Fowler, S. W. (1990). ^{13}C/^{12}C and ^{15}N/^{14}N variations among size-fractionated marine particles: implications for their origin and trophic relationships. *Marine Ecology Progress Series* **59**, 33–8.

Riera, P., and Richard, P. (1996). Isotopic determination of food sources of *Crassostrea gigas* along a trophic gradient in the estuarine Bay of Marennes-Oléron. *Estuarine, Coastal and Shelf Science* **42**, 347–60.

Rochford, D. J. (1972). Nutrient enrichment of east Australian coastal waters. CSIRO Division of Fisheries and Oceanography Technical Paper No. 33.

Shultz, D. J., and Calder, J. A. (1976). Organic carbon ^{13}C/^{12}C variations in estuarine sediments. *Geochimica et Cosmochimica Acta* **40**, 381–5.

Thiel, H., Pfannkuche, O., Schriever, G., Lochte, K., Gooday, A. J., Hemleben, C. H., Mantoura, R. F. G., Turley, C. M., Patching, J. W., and Riemann, F. (1988/1989). Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. *Biological Oceanography* **6**, 203–39.

Thornton, S. F., and McManus, J. (1994). Application of organic carbon and nitrogen stable isotope and C/N ratios as source indicators of organic matter provenance in estuarine systems: evidence from the Tay Estuary, Scotland. *Estuarine, Coastal and Shelf Science* **38**, 219–33.

Thresher, R. E., Nichols, P. D., Gunn, J. S., Bruce, B. D., and Furlani, D. M. (1992). Seagrass detritus as the basis of a coastal planktonic food chain. *Limnology and Oceanography* **37**, 1754–8.

Tranter, D. J., Brandt, S. B., and Cresswell, G. R. (1982). Warm-core eddies shed by the East Australian Current. CSIRO Marine Laboratories Research Report 1979–1981. CSIRO Marine Laboratories Reprint No. 1360.

Walker, A. E., and Wilkin, J. L. (1998). Optimal averaging of NOAA/NASA Pathfinder satellite sea-surface temperature data. *Journal of Geophysical Research* **103**, 12869–83.

Walsh, J. J., Rowe, G. T., Iverson, R. L., and McRoy, C. P. (1981). Biological export of shelf carbon is a sink of the global CO_2 cycle. *Nature* **291**, 196–201.

Wright, S. W., Jeffrey, S. W., Mantoura, R. F. C., Llewellyn, C. A., Bjornland, T., Repeta, R., and Welschmeyer, N. (1991). Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. *Marine Ecology Progress Series* **77**, 183–96.

Manuscript received 4 January 2000; revised and accepted 17 November 2000

Mar. Freshwater Res., 2001, **52**, 463–74

Yellowfin tuna (*Thunnus albacares*) aggregations along the shelf break off south-eastern Australia: links between inshore and offshore processes

J. W. Young, R. Bradford, T. D. Lamb, L. A. Clementson, R. Kloser and H. Galea

Division of Marine Research, CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tas. 7001, Australia

Abstract. In May 1996 the biological oceanography of the main yellowfin tuna longline fishing waters off southern New South Wales, Australia, was examined in relation to the catch by the fishery. A warm-core eddy was identified directly east of Eden with a temperature at 250 m depth of 15°C. At the western edge of this eddy, relatively high levels of fluorescence (chlorophyll *a*) were recorded together with pigments typical of diatoms, a feature of upwelling communities. The biomass of zooplankton and micronekton was also significantly higher at the western edge of the eddy. Similarly, acoustic data showed relatively high concentrations of backscatter at the margins of the eddy, particularly at the shelf break and slope. These areas had the greatest potential prey biomass; a fact supported by the presence of shelf- and slope-associated prey species in the stomachs of yellowfin tuna caught at the same time. Fishery data for yellowfin tuna (*Thunnus albacares*) captures showed that catch per unit effort was highest along the shelf and shelf break. Examination of yellowfin tuna catch records from 1988 to 1998 from south-eastern Australia showed highest catches in 1996, ~75% of the catch coming from the western edge of the eddy. We conclude that the presence of a warm-core eddy in the area at this time provided a localized but productive area to which the yellowfin were attracted.

Introduction

As coastal areas and fronts are the two main sources of nitrogen in oceanic waters, they are commonly the focus of fisheries (Olson *et al.* 1994). Off south-eastern Australia a semi-permanent warm-core eddy forms close to the coast (Cresswell and Legeckis 1986). Both the front around the eddy and the adjacent shelf may provide two sources of nitrogen in close proximity to one another. Perhaps it is for this reason that the area is historically productive and was once the focus of purse seine fisheries for skipjack and southern bluefin tuna (Hynd 1974). At present, there are seasonal longline fisheries for yellowfin (*Thunnus albacares*) and southern bluefin (*Thunnus maccoyii*) tuna in the region. The yellowfin fishery, the focus of this study, runs mainly between April and July, extending along the coast between ~36° and 38°S to 100 n.miles seaward (Australian Fisheries Management Authority database). Its southern extent is restricted by the main front of the East Australia Current.

At these latitudes, however, yellowfin tuna are at the extreme of their range: their main distribution, and the fishery for them, is within tropical waters (Hampton and Gunn 1998). Historical fisheries data indicate that the success (or failure) of some fisheries off south-eastern Australia depends on the strength of the southward flow of tropical waters, which appears to be at its strongest in anti-El Niño (or La Niña) years (Harris *et al.* 1988; Young *et al.* 1993). Consequently, environmental or physical factors may be important determinants of the success of these fisheries from year to year. As tuna are associated with particular oceanic features, similar links could be expected (Sund *et al.* 1981). However, links between the distribution of commercial fish species and oceanographic features have seldom been examined in Australian waters (Healey *et al.* 1990; although see Reddy *et al.* 1994; Lyne *et al.* 1997). As yet, the environment of the southern fishery for yellowfin tuna has not been described. There is, therefore, no way of determining why some years are good for fishing and others bad, or how these years can be related to the regional and biological oceanography of the area. As fishers have ready access to satellite imagery, an understanding of the production and biomass of these waters could also be used to predict productive or non-productive areas and years for this fishery.

Assuming that physical variables such as temperature are within tolerable limits for the tuna, suitable amounts of feed must be an important priority for these high-energy fish. Identifying productive areas therefore may help refine not only our knowledge of broad- and fine-scale tuna movements but also help fishers make best use of their fishing time. Ocean colour imagery (Smith 1981) has been used in the past to identify such productive areas from space, and has helped fishers maximize their fishing effort (Laurs and Fiedler 1985; Fiedler *et al.* 1994). As part of a study to ground-truth ocean-colour data for the east coast of

10.1071/MF99168 1323-1650/01/040463

Australia we made a ship-board survey of the physical and biological oceanography in the area of the tuna longline fishery off south-eastern New South Wales.

In this paper we describe (1) the physical and biological environment of the main yellowfin fishery in eastern Australian waters in May 1996; (2) the distribution of potential prey biomass, estimated from net captures and acoustics; and (3) compare these data with the catch-per-unit-effort of yellowfin tuna in the area.

Methods

In 18–31 May 1996 the CSIRO fisheries research vessel FRV *Southern Surveyor* surveyed the main yellowfin tuna longline fishery off south-eastern New South Wales, Australia (Fig. 1). The physical oceanography of the area was described from two hydrographic transects eastward from the shelf along latitudes 36°25' and 37°15'S (Fig. 1). On each transect, casts of CTDs (General Oceanics Mark IIIC CTD with a General Oceanics 12 bottle rosette and SeaTech fluorometer mounted on the frame) were made at ~10 n.mile intervals to record temperature and salinity to a depth of 1000 m or over the continental shelf to just above the seabed. Fluorescence was measured to a depth of 100 m at each CTD station, and in the surface-water layer while the ship was steaming. Pigment composition and concentration were determined from samples filtered (Whatman GF/F) from 10-L Niskin bottles taken during each CTD cast. The oceanographic data were also used to ground-truth satellite images (from the NOAA AVHRR satellite) of sea-surface temperature.

Net collections

Four types of nets were used to sample the fauna, from microzooplankton (animals <1 mm in length) through macrozooplankton (animals from 1 to 20 mm) to micronekton (animals between 2 and 20 cm) (Omori and Ikeda 1984) (Table 1). At each hydrographic station (Fig. 1) the microzooplankton was sampled with three replicate drop nets (Heron 1982) of mesh size 100 µm and mouth area 0.25 m^2. This net sampled to 100 m, except on the shelf, where it sampled to 60 m. Macrozooplankton was sampled with a paired 70 cm bongo net (mesh size 500 µm) by day. The volume filtered was recorded with a flow meter. A submersible data logger attached to the frame transmitted depth, rate of descent and elapsed fishing time. The bongo net fished obliquely from the surface to 200 m and back again over ~20 min. Over the shelf the bongo was towed to just above the seabed. Micronekton were sampled at night with an IYGPT midwater trawl (Young and Blaber 1986) fitted with an opening/closing codend. The codend used an electronic timer to fire nets at pre-set times. Depth, mouth opening, headline height and board spread of the trawl were monitored acoustically. Sampling consisted of a 40 min oblique tow to 400 m, followed by 15 min stepped-oblique tows at depths of 400–300, 300–200, 200–100 and 100–0 m. A square surface net (mouth area 1 m^2 and 500 µm mesh netting) fitted with a mechanical flow meter was deployed once with each bongo tow and between 2 and 4 times with each midwater trawl. Net samples were usually fixed in 4% formaldehyde in seawater buffered with sodium acetate. However, half of the bongo and all of the surface tows were fixed in ethanol to preserve the otoliths of any fish larva present.

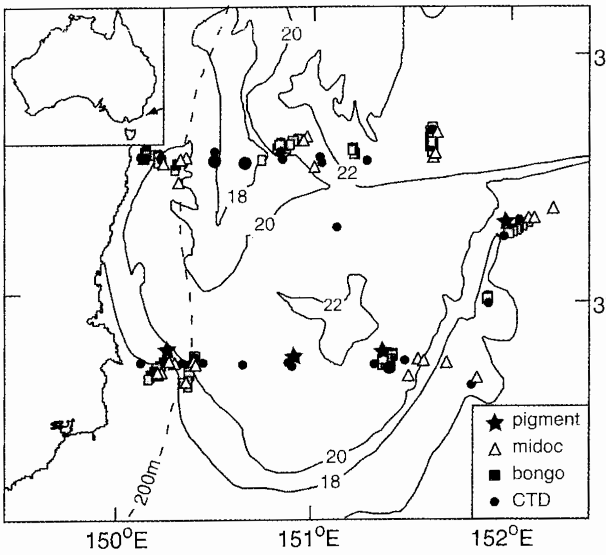


Fig. 1. Study area showing position of CTD casts, midwater trawls and plankton tows off south-eastern New South Wales, Australia, in May 1996. Sea-surface temperature contours were derived from satellite imagery and ground-truthed from CTD data. The acoustic transect came from the Green Cape transect.

Table 1. *Post hoc* Tukey test results for differences in wet weight biomass between areas for both the bongo net (n = 43, d.f. = 39) and surface net data (n = 91, d.f. = 87)

Net	Test condition	m.s.e.	P
Bongo net	Shelf > Front	0.13	0.01
	Shelf > Eddy	0.13	0.00
	Shelf > Slope	0.13	0.00
Surface net	Shelf > Eddy	0.66	0.00
	Slope > Eddy	0.66	0.00
	Front > Eddy	0.66	0.00

Acoustics

A Simrad EK 500 scientific echo sounder was used to collect underway acoustics data to a depth of 400 m, the deepest we sampled. Three frequencies at 12, 38 and 120 kHz with wavelengths at 0.125, 0.0395 and 0.0125 m, respectively, for a sound speed of 1500 m s^{-1} were used. The Simrad EK500 was calibrated with a standard sphere as outlined by Foote (1983) and the data were processed and quality checked following Kloser *et al.* (1996), using a program developed by Waring *et al.* (1994). To avoid changing backscatter due to vertical migration of organisms, the data were grouped by day and night (1.5 h either side of dawn and dusk), allowing time for the organisms to settle. The area backscatter at 38 kHz is presented here for an integrated depth of 20–400 m.

Laboratory and data analysis

Pigment samples were extracted in 90:10 acetone:water and analysed on a Waters high-performance liquid chromatograph, comprising a 600 controller, 717 plus refrigerated autosampler and a 996 photo-diode array detector. Pigments were separated on a stainless steel 25 cm × 4.6 mm I.D. column packed with ODS2 of 5 µm particle size (SGE) with gradient elution, as described in Wright *et al.* (1991). The separated pigments were detected at 436 nm and identified against standard spectra, using Waters Millenium software. Concentrations of chlorophyll *a*, chlorophyll *b*, β,ε-carotene and β,β-carotene in sample chromatograms were determined from standards (Sigma) and all other pigment concentrations were determined from standards of purified pigments isolated from algal cultures. Only data from the dominant pigments are presented here.

The drop, surface and bongo net samples were sorted into fish and zooplankton. A wet weight for each group was recorded. The samples were filtered over a vacuum to remove 'loose' water and weighed (±0.05 g). Trawl samples were sorted to myctophid/stomiform fishes, other fishes, crustacea, squid and gelatinous zooplankton, and weighed (±0.05 g). Micronekton samples were sorted to species where possible, counted and (wet) weighed, although only the major groups are reported here. Crustacean and gelatinous zooplankton were weighed as separate taxa.

The volume filtered by the drop net was calculated by multiplying depth by the area of the mouth opening. The volume filtered (V) by the surface and bongo nets (in m^3) was calculated from the equation $V = D.A$ where D is distance travelled in metres (calculated from mechanical flow meters [General Oceanics Inc.]) and A is net mouth area (m^2). The volume filtered by the Bioness and midoc nets was calculated by the equation $V = S.d.A$, where S is ship's speed ($m\ s^{-1}$) and d is duration of tow (in seconds). Drop net samples were expressed as g (grams wet weight) $10^{-2}\ m^{-3}$. Surface and bongo net samples were expressed as g $10^{-3}\ m^{-3}$, and midoc samples as g $10^{-5}\ m^{-3}$. For all statistical analyses the data were transformed [$\log_e$(standardized total wet weight)] to reduce the variance between the residuals. Analysis of variance (ANOVA) was used to test for a difference between areas. If significant ($P < 0.05$), a *post hoc* Tukey test was used to identify which areas were significantly different from one another.

Yellowfin tuna catch data retrieved from the Australian Fisheries Management Authority for the period 1988–98 included a detailed set for May 1996, when we were at sea. The data are presented as catch per unit effort by weight and number for the region. Size was not recorded, although individual fish weights allowed us to distinguish between different size classes of tuna. As the longline sets were laid along a north–south axis, the data are accurate longitudinally to ± 5 n.miles. However, as the longlines themselves were up to 25 n.miles, we restricted our analyses to longitudinal groupings. Five groups between 150° and 151°45'E were compared by ANOVA, after transformation.

Results

Physical oceanography

The transect east of Bermagui (Fig. 1) identified a thin tongue of southward-flowing East Australia Current water of tropical origin to a depth of ~50 m (Fig. 2). To the south a warm-core eddy, ~60 n.miles in diameter, was situated directly east of Green Cape between 36°30' and 37°30'S and within 10 n.miles of the shelf break (Fig. 1). This eddy had recently separated from East Australian Current waters to the north as demonstrated by previous satellite images of the area (CSIRO, unpublished). It had a mixed layer of 21°C water to a depth of 100 m, and 15°C and a salinity of 35. 4 at 250 m (Fig. 2). Chlorophyll *a* concentrations were highest on the western and south-eastern edges of this eddy (Figs 2 and 3). This was also apparent from the underway sampling of fluorescence, which was lowest in the centre of the eddy (Fig. 3). A strong westerly current (~2 $m\ s^{-1}$) defined the northern boundary of the eddy (Young, personal observation).

Phytoplankton

Chlorophyll *a* concentration in surface waters across the Green Cape transect showed two peaks, one at the shelf (0.62 mg m^{-3}) and one at the north-east edge of the eddy (0.87 mg m^{-3})(Fig. 4*a*). Vertical profiles across the transect show that chlorophyll *a* was at significantly higher levels down to a depth of 40 m at both shelf and offshore stations than at the slope and eddy stations (Fig. 4*c*).

Several pigments are diagnostic markers for specific algal groups (Jeffrey *et al.* 1999), which enables broad identification of the phytoplankton composition in a sample. The three most abundant carotenoids were 19′-hexanoyloxyfucoxanthin (19HF), indicating the presence of prymnesiophytes (e.g. *Phaeocystis* spp.); fucoxanthin, indicating the presence of diatoms (e.g. *Skeletonema* and *Chaetocerus* spp.); and 19′-butanoyloxyfucoxanthin (19BF), indicating the presence of chrysophytes (e.g. *Pelagococcus* spp.) (Fig. 4*b*). On the Green Cape transect, diatoms were dominant only on the shelf, whereas prymnesiophytes were dominant on the slope and at stations within the eddy. Diatoms were also dominant at the offshore station, on the north-east edge of the eddy (Fig. 4*b*).

Biomass of zooplankton and micronekton

Microzooplankton. Microzooplankton biomass ranged from 10.70 (± 1.30 s.e.) g 100 m^{-3} in the eddy to 43.30 (± 10.10 s.e.) g 100 m^{-3} over the slope (Fig. 5), which was significantly different (ANOVA, $n = 62$, $F = 5.70$, $P = 0.00$) (Tukey, m.s.e. = 0.02, d.f. = 58, $P = 0.00$).

Macrozooplankton (depth range 0–200 m). Macrozooplankton were sampled with the bongo net. Because one codend of the bongo net pair was preserved in formalin and the other in alcohol, we compared the wet weight biomass of each side. It was significantly lower in alcohol-preserved samples (t-test, $n = 76$, $P < 0.005$); these samples were therefore multiplied by 1.29 to correct for the difference (t-test, $n = 79$, $P = 0.43$). Left and right codend samples were combined for all subsequent analyses.

Macrozooplankton biomass differed very little between the slope, eddy and frontal areas (all were ~10 g 1000 m^{-3}), but was significantly higher over the shelf (22.62 [± 2.19 s.e.]) g 1000 m^{-3})(Fig. 5, Table 1). Overall, the mean macrozooplankton biomass at the surface was 80.37 [± 8.06 s.e.] g 1000 m^{-3}. Within the eddy, however, biomass was significantly lower (24.60 [± 3.94 s.e.] g 1000 m^{-3}) (Fig. 5) than in the other three areas (ANOVA, $n = 91$, d.f. = 3, $F = 7.13$, $P = 0.00$, Table 1).

Micronekton. The micronekton catch was largely composed of fish, the composition of which changed between inshore and offshore waters. Inshore, jack mackerel (*Trachurus declivis*) dominated the catches; over the slope, lanternfish (*Lampanyctodes hectoris*) dominated. Sonar soundings over the shelf during the day detected large schools of surface and subsurface jack mackerel, identified as such by previous studies in the area (N. Bax, CSIRO, personal communication). Offshore a suite of myctophid

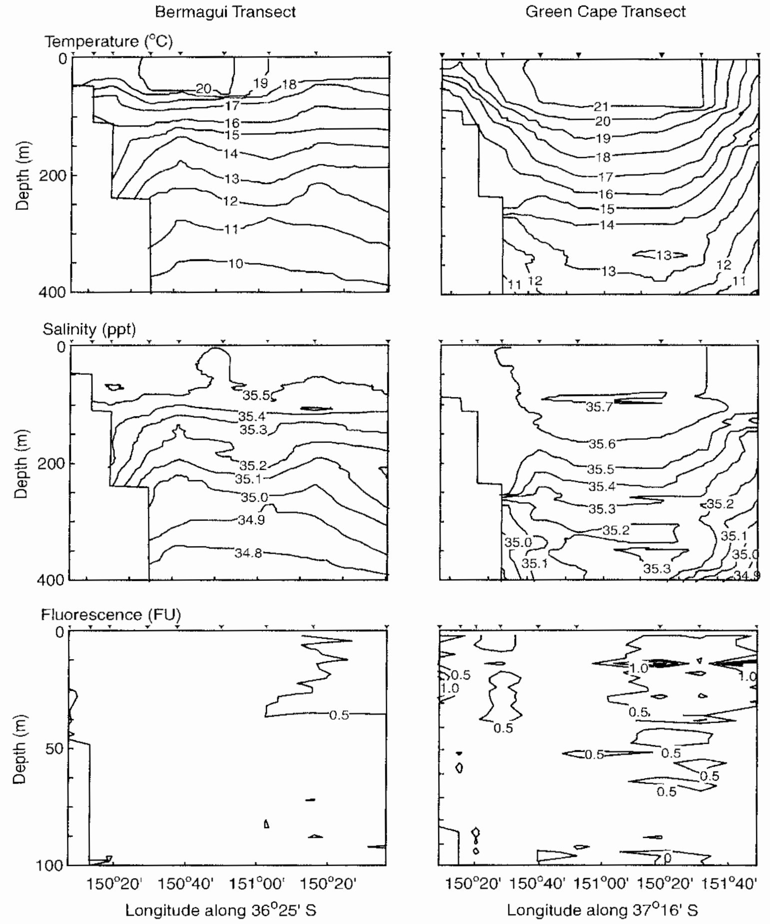


Fig. 2. Vertical cross-sections of the water column to 400 m depth along the two transects completed off south-eastern NSW, Australia, showing temperature, salinity (both to 400 m) and fluorescence (to 100 m depth).

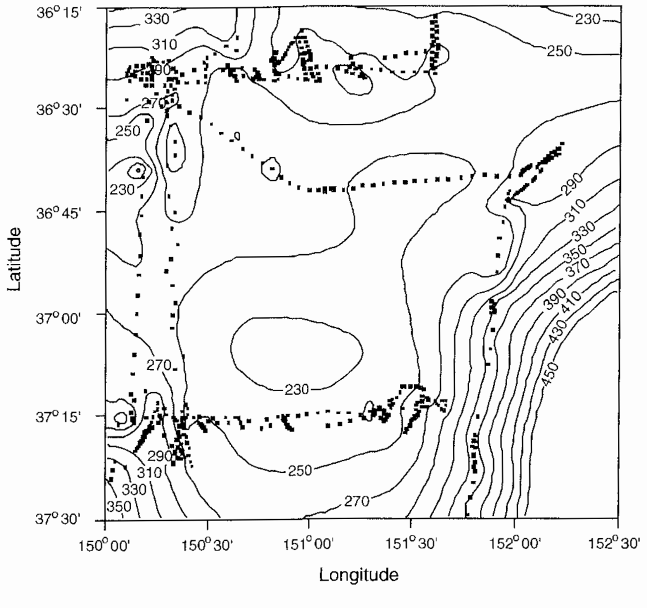


Fig. 3. Contour plot of fluorescence (machine units) constructed from underway sampling taken throughout the cruise.

species, dominated by *Scopelopsis multipunctatus*, and stomiatoid species made up the catches.

The biomass of micronekton over the slope (916.80 ± 488.13 s.e. g 10^5 m^{-3}) was higher than in waters offshore (234.29 ± 7.43 s.e. g 10^5 m^{-3}) (Fig. 5). However, total micronekton biomass was not significantly different between areas (ANOVA, $n = 21$, d.f. = 3, $F = 1.64$, $P = 0.22$). Of the individual taxa, myctophids were significantly more abundant over the slope (ANOVA, $P < 0.01$), whereas Stomiiforme fishes and Crustacea were significantly more abundant offshore (ANOVA, $P < 0.01$) (Fig. 5).

Collectively, the net capture data showed consistently low values on the inside of the eddy, with generally higher biomasses over the shelf break/slope region.

Acoustic data

Distribution of backscatter across the Green Cape transect showed a concentration of backscatter over the shelf and shelf break, a decrease through the eddy but an increase at the eastern edge of the eddy (Fig. 6). The main cause of this

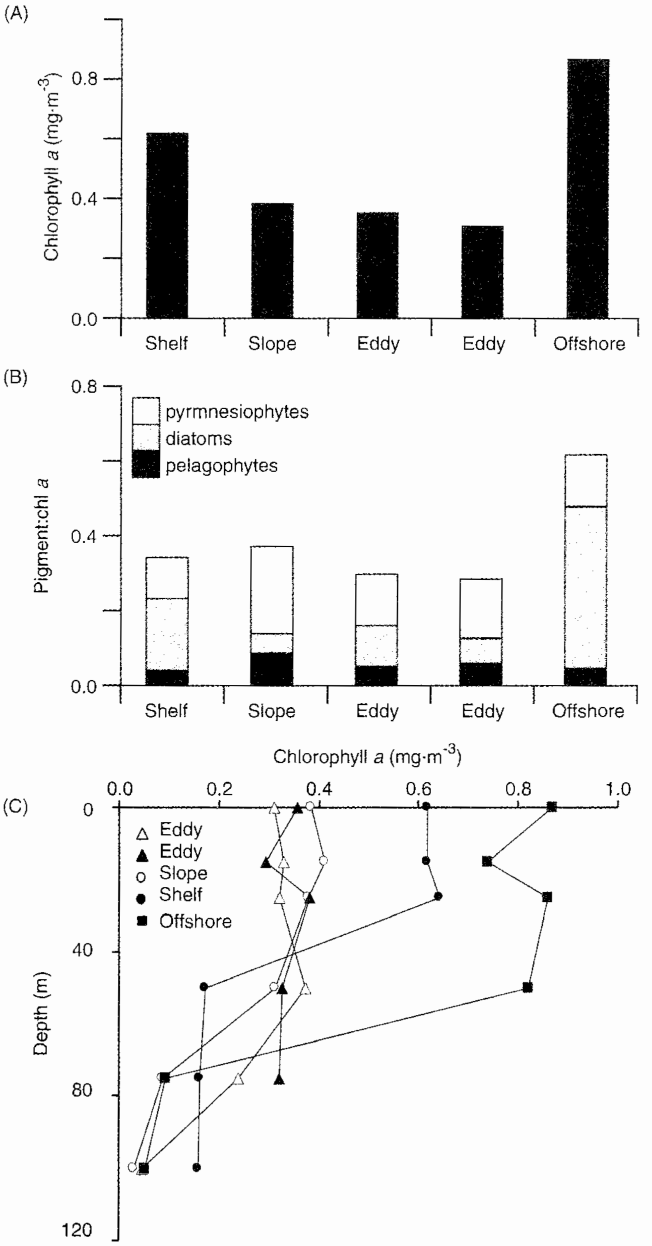


Fig. 4. *(A)* Surface chlorophyll *a*, *(B)* proportion of the main pigment groups and *(C)* depth distribution of chlorophyll *a* across the Green Cape transect.

backscatter is species with gas-filled swimbladders, usually fish species but also squid. In the trawl-sampled species, myctophids and carangids (jack mackerel) dominated, all of which have prominent swim bladders. These groups, which were concentrated over the shelf and slope regions, are also prey of yellowfin tuna (Fig. 5).

Stomach contents of yellowfin tuna

A total of 29 yellowfin tuna stomachs was collected from longline fishers working in the area during the period of the cruise. The yellowfin diet varied widely, but was dominated by fish, squid and crustaceans (Table 2). Of the individual taxa, crab megalopa, species of mackerel and juvenile squid *Notodarus gouldii* dominated the diet (Table 3). Midwater trawling indicated that the mackerel (*Decapterus* spp. and *Trachurus declivis*) were concentrated over the shelf/slope region, whereas the crab megalopa and squid were more common offshore (CSIRO, unpublished).

Fishery data

To examine whether the catches of yellowfin in May 1996 were different from other years we examined 10 years of yellowfin catches by quarter from data obtained from AFMA domestic logbooks for 1988–98 (Fig. 7*a*). In 1996, particularly the second quarter when this study was carried out, catches were significantly higher than in all years except for the same quarter the following year. Further, 73% of all yellowfin tuna caught in the sector during the quarter came from the latitudes encompassing the main eddy (Fig. 7*b*).

In May, yellowfin tuna catches from the study area were significantly different between inshore and offshore waters (ANOVA, $n = 309$, d.f. $= 4$, $F = 3.79$, $P = 0.005$). Catch weight-per-unit-effort was higher close to the shelf break than offshore (Tukey test, $P < 0.01$) (Plate I), although catches rose slightly toward the eastern edge of the eddy. There was a small, but not significant, increase in mean weight (size) off the coast (Plate I). Japanese longliners are excluded from the area of the domestic fishery. However, their catch records for the same period directly east of the domestic fishery showed very few yellowfin catches, but large catches of southern bluefin tuna (*Thunnus maccoyii*), perhaps reflecting the colder water to the east of the eddy (AFMA data base).

Discussion

A persistent warm-core eddy extended below a depth of 400 m adjacent to the coast off south-eastern New South Wales in May 1996. At the western edge of this feature the local domestic longline fishery took about 240 t of yellowfin tuna that month. This was ~75% of the total catch of yellowfin tuna for the month for the east coast of Australia. Further, catch records from 1988 to 1998 from south-eastern Australia showed that one of the highest catches of yellowfin tuna occurred during this period (May 1996). Our data indicate that these aggregations were related to the regional oceanography at that time.

Physical and biological oceanography

The edges of the eddy had closely spaced upward-sloping isotherms, which indicated upwelling and possible nutrient enrichment, particularly along the shelf break where eddy waters appeared to intrude onto the shelf. Similar eddy-generated coastal enrichments have been reported

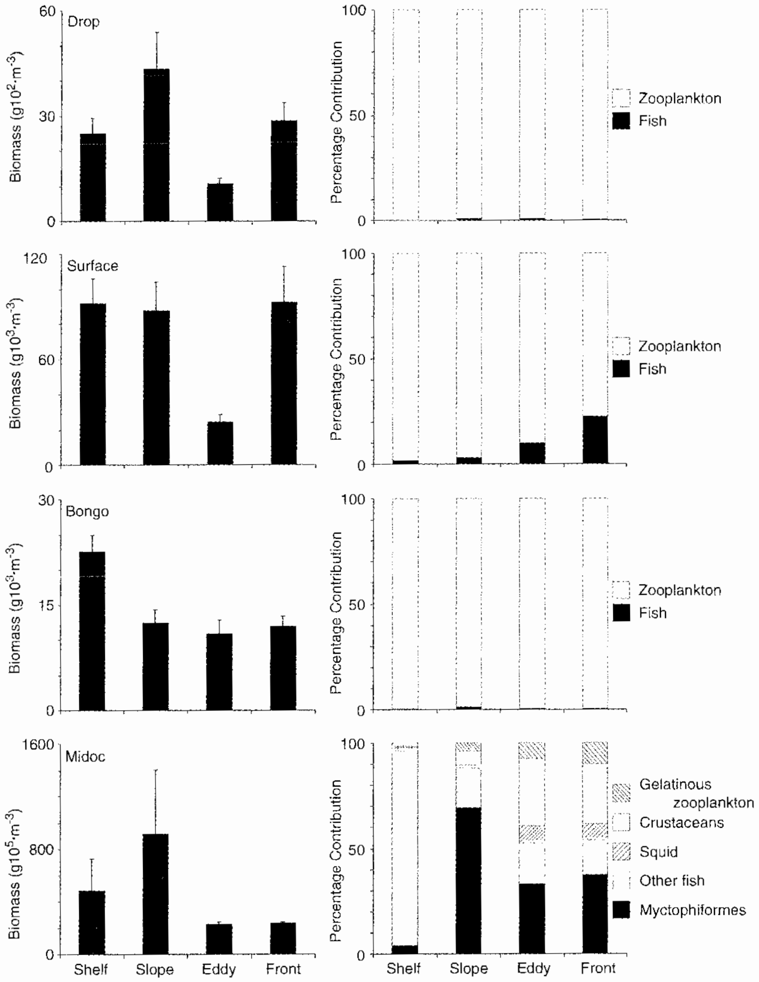


Fig. 5. Biomass of microzooplankton (g $10^{-2}m^{-3}$), macrozooplankton (g $10^{-3}m^{-3}$) and micronekton (g $10^{-5}m^{-3}$) from the shelf, slope, eddy and offshore of the study area. The percentage contributions of the wet weight of contributing taxa are presented for each net type.

previously along the coast of NSW (Tranter *et al.* 1983, 1986; Cresswell 1994), and from elsewhere (e.g. Paffenhofer *et al.* 1987). Cresswell (1994) gave an elaborate description of how the southward component of a warm-core eddy close to the coast off central NSW drove 'an Ekman bottom boundary layer shoreward, where it upwelled to the surface', generating very high fluorescence values.

However, not all upwelling events necessarily lead to increased concentrations of potential feed for tuna. Tilstone *et al.* (1999) summarize the many factors (including, but not limited to, upwelling strength and persistence, stratification, wind strength and water column heating) that must combine for primary productivity to increase. It then requires phytoplankton of suitable size for a 'classic' food web to develop (Cushing 1989). That is, the main pathway of biomass transfer from plankton to fish is via diatoms to meso/macrozooplankton to fish (see Robinson 1994 for review). This is based on the view that smaller-sized phytoplankton (i.e. <5 μm) are eaten by protozoans, whereas larger species (diatoms) are eaten by metazoans such as copepods and euphausiids, which in turn form the basis of many coastal fisheries (Kiorboe 1993). In this study we found not only one of the highest levels of chlorophyll *a* at the shelf edge, but the highest concentration of fucoxanthin, indicating a dominance of diatoms in the phytoplankton composition in these waters. Our data indicate that the physical and biological conditions had been sufficiently persistent for a localized food chain to develop.

Phytoplankton fluorescence

As no ocean colour imagery was available at the time (the Japanese ocean colour satellite ADEOS was not launched until August 1996, the NASA ocean colour satellite in

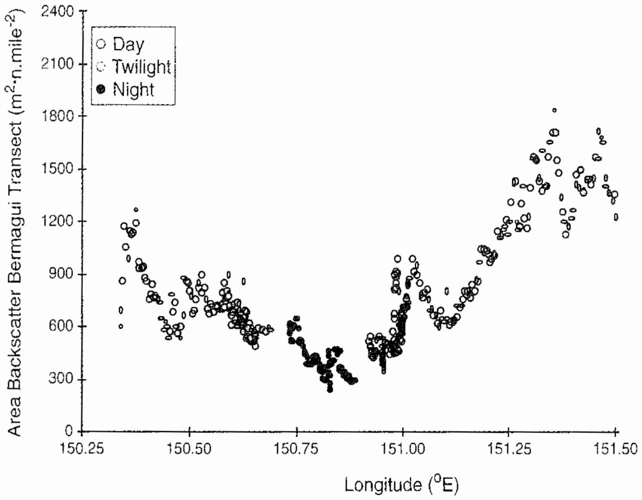


Fig. 6. Integrated area backscatter (m^{2}n.mile^{-2}) from 20 to 400 m separated into day, night and twilight along the Green Cape transect from the continental shelf seaward off south-eastern NSW.

September 1997), we constructed a fluorescence 'map' from our underway sampling (Fig. 3). Fluorescence maxima were found at the eastern and western edges of the eddy similar to that observed in the vertical cross sections of fluorescence and temperature across the eddy. Fluorescence and temperature fronts do not always correspond (Fiedler *et al.* 1994), although this is usual in upwelling zones off California (Fiedler and Barnard 1987). That the highest catch per unit effort data was closely linked to the productive area of the study adds further support to the relationship.

Net captures of potential prey

Our net sampling indicated that, overall, biomass was concentrated over the shelf or just outside over the continental slope. We noted also that the species composition, particularly of the micronekton, shifted from a myctophid/stomiform mix offshore to one dominated by shelf-associated species such as carangids inshore. Estimates from nets of potential prey species can significantly underestimate their biomass (Koslow *et al.* 1997), because faster or larger prey can avoid the net and smaller prey can escape from it. However, sampling with a range of nets minimizes the bias (Young *et al.* 1996). 'Catchable' species such as myctophids are generally associated with pelagic fauna, particularly cephalopods, that are both difficult to catch and also potential prey of the tuna (Auster *et al.* 1992). Further, studies of zooplankton species within food webs leading to tuna have shown that tropical tuna are more concentrated where these prey species are more concentrated (Roger 1994).

Acoustic data

Acoustic backscatter was highest at the western and eastern edges of the eddy. This increase in backscatter was reflected in the net data, particularly at the western edge/slope region where net biomasses were generally highest. Although no fishery data are available for the eastern edge, the catches from the western side showed that the highest catches of tuna occurred where the acoustic backscatter was highest. Although the relationship between sound scattering layers and potential prey species of larger predators such as tuna is well known (e.g. Marchal *et al.* 1993), it is only recently that studies are beginning to link the presence of these scattering layers with the larger predators. Bertrand *et al.* (1999) found that tuna distributions off French Polynesia were directly linked to food availability, the density of which could be assessed by echo-sounding. Similarly, Fiedler *et al.* (1998) found that dolphin-sighting rates were correlated positively with night-time volume scattering strength above the thermocline. Marchal *et al.* (1993) extended this relationship between 'acoustic biomass' and 'trophic abundance' to concentrations of potential prey of yellowfin tuna in the eastern Atlantic, a similar relationship to that found in the present study.

Fishery data

It could be argued that the yellowfin tuna catches, our indicator of their distribution, were a function of the inability of the boats to fish further seaward and not of the concentration of fish. However, tuna fishers usually concentrate where catches are favourable (Calkins 1961; Keene and Pearcy 1976), that is, fleet distributions reflect fish distribution to some degree (Healey *et al.* 1990). This may be the case off south-eastern NSW, although we suspect that yellowfin tuna might also have been at the eastern edge of the eddy.

The research cruise coincided with one of the two highest overall catches of yellowfin tuna for the NSW coast between 1988 and 1998. Catches for that month and the other high catch month (May 1997) were ~3 times that of any other period (and one of the highest catch rates). Furthermore, three-quarters of the catch for each period came from between latitudes 35 and 37 degrees south. There is no evidence that the presence of the eddy was the reason for the high catches overall, but the oceanographic

Table 2. Proportions of the major taxa in the stomachs of yellowfin tuna (n = 39) caught off south-eastern New South Wales in May 1996

%*n*, percentage of total number containing prey; %*w*, percentage of total weight; %*f*, percentage frequency of occurrence of individual prey species in the stomachs examined

	%*n*	%*w*	%*f*
Crustacea	72.15	6.18	58.62
Cephalopoda	19.65	14.16	72.41
Pisces	6.89	79.35	93.10
Others	1.31	0.32	17.24

Table 3. Prey composition of stomach contents of yellowfin tuna ($n = 39$) caught off south-eastern New South Wales during the period of the research cruise (SS3/96) in May 1996
See Table 2 for definitions

		Prey	%*n*	%*w*	%*f*
Crustacea					
	Amphipoda				
		Unidentified amphipods	0.07	0.02	3.45
		Brachyscelus crusculum	0.15	0.02	6.9
		Platyscelus ovoides	0.22	0.02	6.9
	Decapoda				
		Crab megalopa	71.5	6.1	55.17
		Scyllarus crenatus	0.07	<0.01	3.45
	Unidentified		0.15	0.01	6.9
Mollusca					
	Pteropoda				
		Cavolinia sp.	0.8	0.21	6.9
	Cephalopoda				
		Argonauta sp.	0.15	0.27	3.45
		Nototodarus gouldi	1.38	13.27	31.03
		Todarodes filipovae	0.07	0.03	3.45
		Unidentified Ommastrephidae	0.36	<0.01	13.79
		Unidentified squid	0.22	0.2	10.34
		Juvenile squid beaks	15.08	0.24	48.28
		Squid beaks	2.39	0.15	24.14
Tunicata					
		Unidentified salp	0.07	0.01	3.45
		Amphipod barrels	0.44	0.1	6.9
Pisces					
		Balistidae	0.07	0.1	3.45
		Brama sp.	0.07	0.44	3.45
		Carangidae	0.29	11.27	13.79
		Decapterus sp.	0.29	30.28	6.9
		Diodontidae	0.07	<0.01	3.45
		Gempylidae	0.15	1.91	6.9
		Hemiramphidae	0.73	11.4	17.24
		Lactoria sp.	0.07	0.01	3.45
		Fish larvae	0.58	0.08	6.9
		Monacanthidae	0.65	3.25	20.69
		Nemichthyidae	0.07	0.01	3.45
		Ostraciidae	1.23	0.37	6.9
		Sardinops neopilchardus	0.07	2.81	3.45
		Scomberesox saurus	0.22	2.36	6.9
		Scopelosaurus sp.	0.07	0.14	3.45
		Symbolophorus sp.	0.07	0.36	3.45
		Tetraodontidae	0.87	5.06	31.03
		Tetrasomus concantenatus	0.65	0.3	13.79
		Trachurus sp.	0.22	9.06	10.34
		Unidentified fish	0.44	0.14	17.24

conditions may have initially attracted and encouraged what appeared to be a pulse of yellowfin to stay in this particularly productive area. As this cruise was a one-off study, we effectively have no control with which to test whether the conditions off Eden were unique below the surface. However, examination of the satellite imagery for May 1997, the other high catch period, shows a similar pattern, that is, an anticyclonic warm-core eddy near the coast at the same latitudes.

Yellowfin tuna distributions in relation to feed and temperature

The perception that tuna aggregate in areas of greater potential feed is not new. For example, Roger (1994) found that the biomass of viable forage was a key factor in controlling the abundance and distribution of yellowfin in the tropics. Specifically, he found that the biomass of suitable plankton in 'good' yellowfin fishing areas was seven times higher than in poor fishing areas. Fiedler and

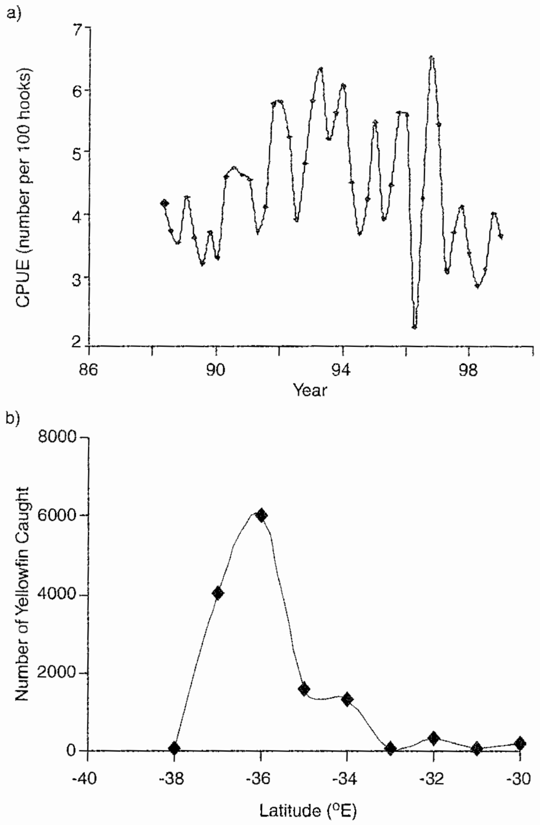


Fig. 7. *(a)* Catch per unit effort (number per hundred hooks) of yellowfin tuna (*Thunnus albacares*) off south-eastern NSW between 1988 and 1998; and *(b)* number of yellowfin tuna caught along the NSW coast by degree of latitude in the second quarter of 1996.

Barnard (1987) found that albacore tuna (*Thunnus alalunga*) and skipjack (*Katsuwonus pelamis*) were 'feeding near mesoscale centres of high productivity where prey abundance may be enhanced' off California. Such investigations indicate that the tuna were coming to (and staying in) areas in which their prey was concentrated, a conclusion reached in the present study. Although limited in number, the stomachs examined contained a high proportion of shelf or slope associated prey species, particularly pilchards, carangids and monacanthids.

It is unlikely that prey levels were the only reason for the tuna's presence in the area. In the Northern Hemisphere, yellowfin tuna are restricted by their temperature tolerance to warmer waters (Block *et al.* 1997). Further, even when these fish do move further north into colder waters (in summer and autumn) to take advantage of higher prey abundance, they remain for most of the time in the warmer surface waters (Block *et al.* 1997). The waters of the outlying Tasman Sea at the latitude of this study are well below the temperature of the yellowfin's usual thermal range. Therefore, without the presence of the East Australia Current at this latitude it is unlikely that yellowfin tuna would be found in the area, regardless of prey concentration. The East Australia Current extends southward past this point, to the southern tip of Tasmania, but with diminishing size, depth and temperature (Young *et al.* 1996). Off Eden the East Australia Current was as much as 22 °C during May 1996, whereas at the same time off Tasmania it was only 17 °C (CSIRO, SST archive). Only during out-of-the-ordinary intrusions of warm water along the Tasmanian coast (as in La Niña periods) are yellowfin tuna taken in any numbers off eastern Tasmania (Young 1998), even though potential prey species are equally or more abundant than off the New South Wales coast (Young *et al.* 1997). We conclude therefore that the combination of the warmer water of the eddy/East Australia Current and the aggregations of the prey species at its boundaries maintained the concentrations of yellowfin tuna at a latitude outside their 'normal' range.

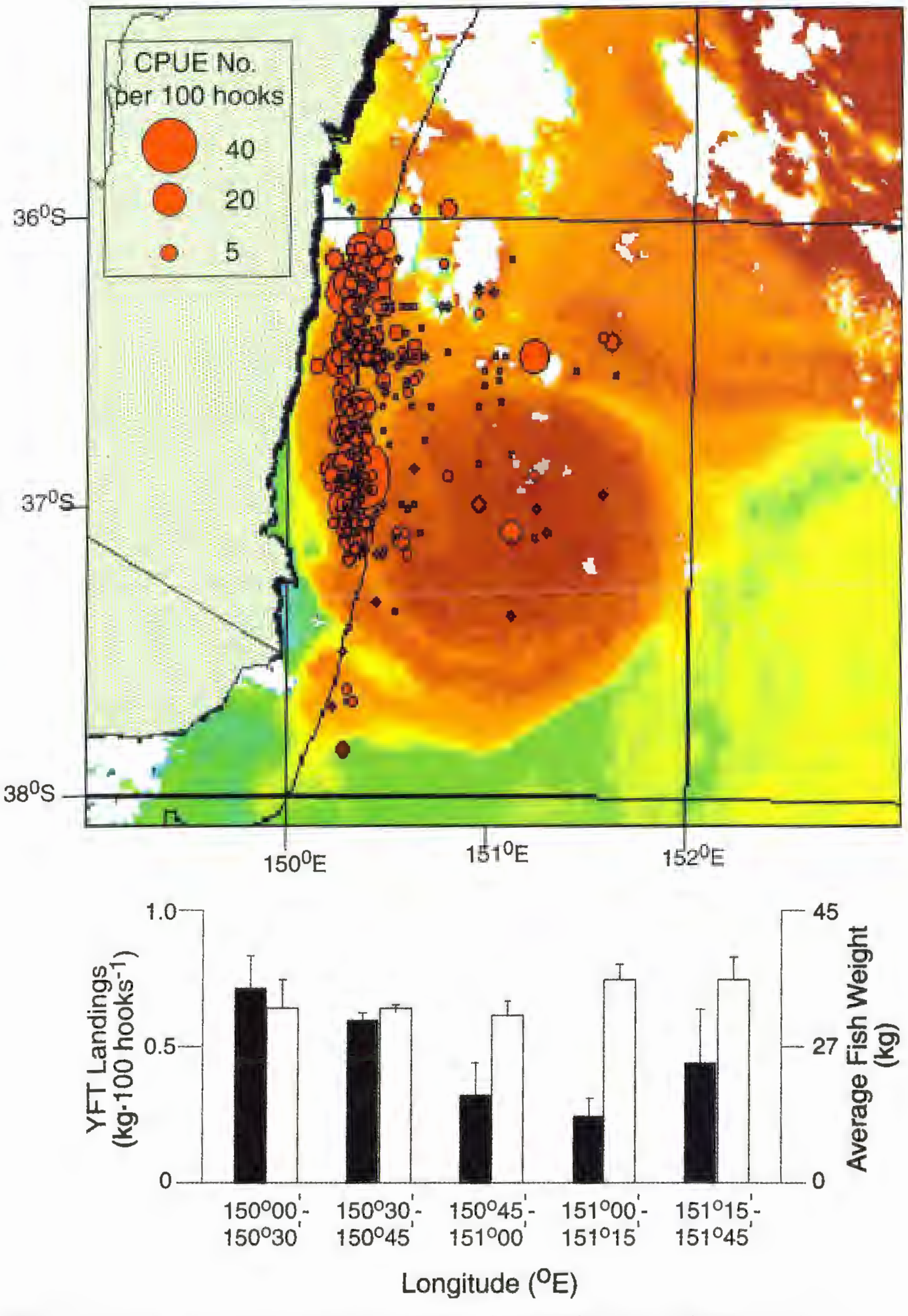


Plate I. Catch per unit effort (numbers per 100 hooks) of yellowfin tuna (*Thunnus albacares*) in relation to sea surface temperature off south-eastern New South Wales in May 1996. The histogram shows CPUE (weight in kg per 100 hooks, closed histograms) and average fish weight (in kg, open histograms) in relation to longitude.

Acknowledgments

We thank the longline fishers from Bermagui and Eden for their cooperation with this project. Yellowfin tuna catch data were retrieved from the AFMA database. This work was partly funded by FRDC grant 94/45 to study the relationship between 'ocean colour' satellite imagery and ocean processes off eastern Australia. Drs Alan Williams, Cathy Bulman, John Gunn (CSIRO Marine Research) and Alan Jordan (Tasmanian Aquaculture and Fisheries Institute) made useful suggestions on the manuscript.

References

Auster, P. J., Griswold, C. A., Youngbluth, M. J., and Bailey, T. G. (1992). Aggregations of myctophid fishes with other pelagic fauna. *Environmental Biology of Fishes* **35**, 133–9.

Bertrand, A., Le Borgne, R., and Josse, E. (1999). Acoustic characterisation of micronekton distribution in French Polynesia. *Marine Ecology Progress Series* **191**, 127–40.

Block, B. A., Keen, J. E., Castillo, B., Dewar, H., Freund, E. V., Marcinek, D. J., Brill, R. W., and Farwell, C. (1997). Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Marine Biology* **130**, 119–32.

Calkins, T. P. (1961). Measures of population density and concentration of fishing effort for yellowfin and skipjack tuna in the eastern tropical Pacific Ocean. 1951–1959. Inter-American Tropical Tuna Commission Bulletin No. 6, 69–152.

Cresswell, G. (1994). Nutrient enrichment of the Sydney continental shelf. *Australian Journal of Marine and Freshwater Research* **45**, 677–91.

Cresswell, G. R., and Legeckis, R. (1986). Eddies off south-eastern Australia. *Deep-Sea Research* **33**, 1527–62.

Cushing, D. H. (1989). A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *Journal of Plankton Research* **11**, 1–13.

Fiedler, P. C., and Barnard, H. J. (1987). Tuna aggregations and feeding near fronts observed in satellite imagery. *Continental Shelf Research* **7**, 871–81.

Fiedler, P. C., Smith, G. C., and Laurs, R. M. (1994). Fisheries applications of satellite data in the eastern North Pacific. *Marine Fisheries Review* **46**, 1–13.

Fiedler, P. C., Barlow, J, and Gerrodette, T. (1998). Dolphin prey abundance determined from acoustic backscatter data in eastern Pacific surveys. *Fishery Bulletin* **96**, 237–47.

Foote, K. G. (1983). Maintaining precision calibrations with optimal copper spheres. *Journal of the Acoustical Society of America* **73**, 1054–63.

Hampton, J., and Gunn, J. (1998). Exploitation and movements of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) tagged in the north-western Coral Sea. *Marine and Freshwater Research* **49**, 475–89.

Harris, G. P., Davies, P., Nunez, M., and Meyers, G. (1988). Interannual climate variability in Tasmania and its effects on freshwater and marine fisheries. *Nature (London)* **333**, 754–7.

Healey, M. C., Thomson, R. E., and Morris, J. F. T. (1990). Distribution of commercial troll fishing vessels off southwest Vancouver Island in relation to fishing success and oceanic water properties and circulation. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1846–64.

Heron, A. (1982). A vertical free fall net with no mouth obstruction. *Limnology and Oceanography* **27**, 380–3.

Hynd, J. S. (1974). Unusual bluefin tuna season in NSW. *Australian Fisheries* (April), 9–11.

Jeffrey, S. W., Wright, S. W., and Zapata, M. (1999). Recent advances in HPLC pigment analysis of phytoplankton. *Marine and Freshwater Research* **50**, 879–96.

Keene, D. F., and Pearcy, W. G. (1976). Comparison of the most successful and least successful west coast albacore troll fishermen. *Fishery Bulletin* **74**, 973–82.

Kiorboe, T. (1993). Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advances in Marine Biology* **29**, 1–61.

Kloser, R. J., Koslow, J. A., and Williams, A. (1996). Acoustic assessment of the biomass of a spawning aggregation of orange roughy (*Hoplostethus atlanticus*, Collett) off south-eastern Australia, 1990–93. *Marine and Freshwater Research* **47**, 1015–24.

Koslow, A. J., Kloser, R. J., and Williams, A. (1997). Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. *Marine Ecology Progress Series* **146**, 21–35.

Laurs, R. M., and Fiedler, P. C. (1985). Application of satellite remote sensing to US fisheries. In 'Oceans '85 Proceedings: Ocean Engineering and the Environment'. 1985, **1**, pp. 320–3, OCEANS '85.

Lyne, V. D, Scott, R. A., Gray, R. C., and Bradford, R.W. (1997). Quantitative interpretation of fine-scale catch-per-unit-effort for southern bluefin tuna off southeast Australia. Final Report for Fisheries Research Development Corporation Project 93/077.

Marchal, E., Gerlotto, F., and Stequert, B. (1993). On the relationship between scattering layer, thermal structure and tuna abundance in the eastern Atlantic equatorial current system. *Oceanologia Acta* **16**, 261–73.

Olson, D. B., Hitchcock, G. L., Mariano, A., Ashjian, C. J., Peng, G., Nero, R. W., and Podesta, G. P. (1994). Life on the edge: marine life and fronts. *Oceanography* **7**, 52–60.

Omori, M., and Ikeda, T. (1984). 'Methods in Marine Zooplankton Ecology.' (Wiley: New York.) 332 pp.

Paffenhofer, G. A., Atkinson, L. P., Blanton, J. O., Lee, T. N., Pomeroy, L. R., and Yoder, J. A. (1987). Summer upwelling on the southeast continental shelf of the USA during 1981: summary and conclusions. *Progress in Oceanography* **19**, 437–41.

Reddy, R., Lyne, V. Gray, R., Easton, A., and Clarke, S. (1994). An application of satellite-derived sea surface temperatures to southern bluefin tuna and albacore off Tasmania, Australia. *Scientia Marina* **59**, 445–54.

Robinson, C. L. K. (1994). The influence of ocean climate on coastal plankton and fish production. *Fisheries Oceanography* **3**, 159–71.

Roger, C. (1994). The plankton of the tropical western Indian Ocean as a biomass indirectly supporting surface tunas (yellowfin, *Thunnus albacares* and skipjack, *Katsuwonus pelkamis*). *Environmental Biology of Fishes* **39**, 161–72.

Smith, R. C. (1981). Remote sensing of depth distribution of ocean chlorophyll. *Marine Ecology Progress Series* **5**, 359–61.

Sund, P. M., Blackburn, M., and Williams, F. (1981). Tunas and their environment in the Pacific Ocean: a review. *Oceanography and Marine Biology Annual Review* **19**, 443–512.

Tilstone, G. H., Figuerias, F. G., Fermin, E. G., and Arbones, B. (1999). Significance of nanoplankton photosynthesis and primary production in a coastal upwelling system (Ria de Vigo, NW Spain) *Marine Ecology Progress Series* **183**, 13–27.

Tranter, D., Leech, G., and Airey, D. (1983). Edge enrichment in an ocean eddy. *Australian Journal of Marine and Freshwater Research* **34**, 665–80.

Tranter, D. J., Carpenter, D. J., and Leech, G. S. (1986). The coastal enrichment effect of the East Australia Current eddy field. *Deep-sea Research* **33**, 1705–28.

Waring, J. R., Kloser, R. J., and Pauly, T. (1994). 'ECHO'-Managing Fisheries Acoustic Data. In 'Proceedings of the International Conference on Underwater Acoustics; 1994 Dec; University of New South Wales. Darling Public School, NSW, Australia'. pp. 22–4. (Australian Acoustic Society.)

Wright, S. W., Jeffrey, S. W., Mantoura, R. F. C., Llewellyn, C. A., Bjørnland, T., Repeta, D., and Welschmeyer, N. (1991). Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. *Marine Ecology Progress Series* **77**, 183–96.

Young, J. W. (1998). The ecology of midwater fish and zooplankton from coastal and oceanic waters of eastern Tasmania, Australia. PhD Thesis, University of Tasmania. 145 pp.

Young, J. W., and Blaber, S. J. M. (1986). Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. *Marine Biology* **93**, 147–56.

Young, J. W., Jordan, A. R., Bobbi, C., Johannes, R. E., Haskard, K., and Pullen, G. (1993). Seasonal and interannual variations in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern Tasmania, Australia. *Marine Biology* **116**, 9–18.

Young, J. W., Bradford, R. W., Lamb, T. D., and Lyne, V. D. (1996). Biomass of zooplankton and micronekton in the southern bluefin tuna fishing grounds off eastern Tasmania, Australia. *Marine Ecology Progress Series* **138**, 1–14.

Young, J. W., Lamb, T. D., Le, D., Bradford, R., and Whitelaw, A. W. (1997). Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. *Environmental Biology of Fishes* **50**, 275–91.

Manuscript received 19 November 1999; revised and accepted 18 September 2000

Mar. Freshwater Res., 2001, **52**, 475–89

Remote sensing of seabed types in the Australian South East Fishery; development and application of normal incident acoustic techniques and associated 'ground truthing'

R. J. Kloser, N. J. Bax, T. Ryan, A. Williams and B. A. Barker

CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia. email: rudy.kloser@marine.csiro.au

Abstract. Calibrated acoustic backscattering measurements using 12, 38 and 120 kHz were collected over depths of 30–230 m, together with benthic epi- and in-fauna, sediments, photographs and video data. Each acoustic ping was envelope detected and digitized by echo sounder to include both the first and second echoes, and specifically designed software removed signal biases. A reference set of distinct habitat types at different depths was established, and a simple classification of the seabed combined both biological and geological attributes. Four seabed types were identified as having broad biological and geological significance; the simple acoustic indices could discriminate three of these at a single frequency. This demonstrates that the acoustic indices are not directly related to specific seabed properties but to a combination of seabed hardness and roughness attributes at a particular sampling frequency. The acoustic-derived maps have greater detail of seabed structure than previously described by sediment surveys and fishers' interpretation. The collection of calibrated digital acoustic data at multiple frequencies and the creation of reference seabed sites will ensure that new shape- and energy-based feature extraction methods on the ping-based data can begin to unravel the complexities of the seabed. The methods described can be transferred to higher-resolution swath-mapping acoustic-sampling devices such as digital side-scan sonars and multi-beam echo sounders.

Introduction

The present day seabed is a mix of recent biological, hydrological and chemical processes layered over a geological framework developed through the eons. Both the seabed and the invertebrate and fish communities are structured by depth, sediment types, latitude and hydrological processes (e.g. Snelgrove and Butman 1994; Coleman *et al.* 1997). However, the links between seabed landscape, or 'seascape', and animal communities are frequently not well described because of the difficulty of sampling broad areas of the seabed, especially over rough ground and at depth. In a recent study of the south-east Australian continental shelf, the relationships between animal communities and seabed type were established from point (or transect) samples by using a variety of fixed and mobile fishing gears, underwater photography and physical samplers (Bax and Williams 2000). Vertical sounding acoustics were used to determine where these samples should be taken and to provide maps of seabed types to generalize from point (or transect) samples to the broader shelf area. In this paper we describe the validation and results of that acoustic mapping.

Shape and energy features from the range corrected, enveloped acoustic signals obtained with normal incident high frequency narrow band acoustic systems have been used to characterize the seabed (Orlowski 1984; Chivers *et al.* 1990; Lurton and Pouliquen 1992; Collins *et al* 1996). Seabed descriptions have been based on simple analysis of both the first and second reflected echoes (Orlowski 1984; Chivers *et al.* 1990), or on detailed analysis of the first echo alone (Lurton and Pouliquen 1992; Collins *et al.* 1996). Fishers use similar features in their own seabed mapping. However, whereas it is clear that these descriptors provide relative information on the features (hardness and roughness) of adjacent seabed types at similar depths, or on particular prominent outcrops, it is not clear that these same descriptors can provide seabed descriptors that are consistent in different areas and over a wide range of depths (Bax *et al.* 1999).

The seabed of the south-east Australian shelf can be described using basic physical and biological properties such as soft, hard, rough and smooth seabed features. Using this approach, Bax *et al.* (1999) showed that relatively simple acoustic indices can produce biologically significant seabed characterization over a limited depth range, 40–60 m, although they noted a possible depth bias in the indices. This possible depth bias was a concern when extending the method to the depth range of the continental shelf in this area, 30–230 m. Previous researchers using commercial

10.1071/MF99181 1323-1650/01/040475

equipment — the RoxAnn system based on the classification scheme of Chivers *et al.* (1990) — to classify seabed type, have operated over narrow depth ranges (Magorrian *et al.* 1995; Kaiser *et al.* 1998) or found a possible depth bias (Greenstreet *et al.* 1997). Furthermore, data quality problems (Greenstreet *et al.* 1997) and biases due to varying ship speed (Magorrian *et al.* 1995) have been reported.

Clearly, we needed to establish the depth dependency in our data before we applied a general classification scheme over our wide depth range. Also, we needed to maintain data quality when trying to combine data recorded in a variety of sea states, from a number of surveys and with different instrument configurations. For these reasons we used a scientific echo-sounder that stores a digital record of the acoustic reflection from each acoustic ping. These raw data are re-analysed in this paper to determine the biases associated with sampling at different depths, and sea conditions. We apply simple energy-based feature extractions of the first and second seabed echoes following the techniques of Chivers *et al.* (1990). Extracted acoustic features are then compared with the ground-truth data obtained from a set of 10 reference seabed types that were also sampled with sediment grab, benthic dredge, photographic and video samplers. Finally, maps of the acoustic features are compared with sediment and fishers' interpretation maps of the region.

Material and methods

Study area

The study region was a section of the south-east coast of Australia between 36° and 39°S (Fig. 1). In this region, the shelf extends to ~170–200 m depth and is 25 km wide in the north of the study region and over 175 km wide in the south. The seabed is a complex patchwork of massive sediment mosaics with limestone reefs, granite and sandstone bedrocks, and consolidated sediments outcropping in prominent tracts and dispersed patches (Bax and Williams 2000). In overview, the inner-shelf sediment plains of the western section are studded with patches of mostly low-relief limestones and sandstones, whereas to the east, smaller sediment plains are bounded mid-shelf by an elongated buttress of limestone patch reefs. In the eastern regions, sediment plains of the inner and outer shelf are bounded by the largest tract of hard-ground on the south-eastern shelf, the mosaic of limestone reefs forming the Gabo/Howe Reef complex. The shelf break is marked by structurally complex features formed by the necks of the Bass Canyon. Our sampling combined low intensity sampling over a broad area (as shown by the vessel tracks in Fig. 1) and intensive sampling targeted in areas of heterogeneous seabed (mesohabitats in Fig. 1).

Reference seabed types

We 'calibrated' or ground-truthed our interpretation of acoustic data by intensively sampling 10 reference sites with multi-frequency acoustics and physical samplers. A range of reference sites was selected that provided contrasts in seabed type and depth; these were situated within 'mesohabitat' study areas known to have heterogeneous substrata with a variety of associated epibenthic communities (Bax and Williams 2000). The data evaluated for each reference site included acoustic indices and echograms, seabed depth and position, photographic imagery, identification of sediment-type or lithology, and epibenthic community type (Table 1). A flow diagram of the data collection and processing from the various samplers is shown in Fig. 2.

Figure 1

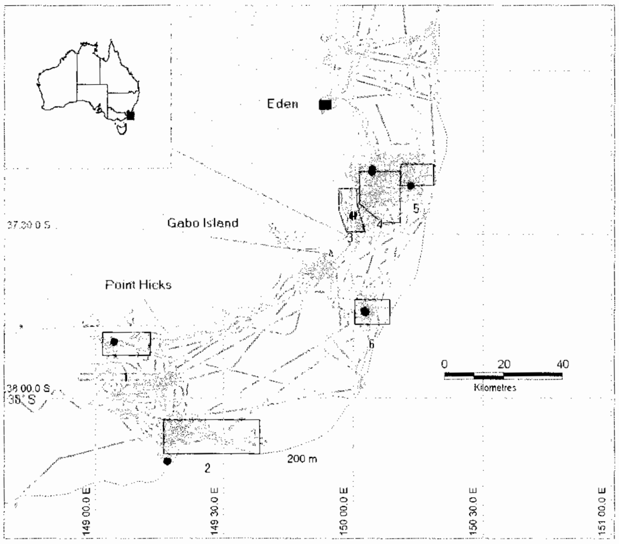


Fig. 1. Map of the South East Fishery (SEF) region for the ecosystem study, with mesohabitats and the vessel tracks where acoustic data were collected for voyages in April and December 1996. Mesohabitats (10s of metres to 1 km) are 1, Point Hicks; 2, Horseshoe; 3, Black Head; 4, Disaster Bay; 5, Big Gutter; 6, Gabo Reef. Reference sampling sites are highlighted with dots.

Biological, physical and visual sampling

Invertebrate epifauna and infauna were collected with a large benthic dredge along transects of approximately 1200 m length (corresponding to a tow speed of ~1 m s^{-1} for 20 min). Our assessment of community type was based on these biological samples in conjuction with photographic images. We used two camera systems to provide image data: a 35 mm Photosea camera mounted on the benthic sled, and a video camera on a towed platform (Barker *et al.* 1999). The towed video platform was particularly useful over rough ground that could not be sampled by the sled. Images were taken at 12 s intervals (~12 m) during sled transects. Sediments were collected initially by a Smith McIntyre grab, but subsequently by a pipe dredge, and a collecting box situated on one skid of the benthic sled, because of the loss of the grab. The mean grain size for each sample was calculated by the method of moments (Folk 1968). Rock samples were collected opportunistically from the benthic sled and fishing gears and classified from slabs and thin-sections (Bax and Williams 2000).

Normal incident acoustics

Plate 1 shows the normal incident narrow conical beam sounding technique and the process of formulation of the first and second echo. The displayed echogram represents a recording of the returned echoes from repeated individual acoustic pulses. The acoustic waveform of the returned echo is band-passed and the squared echo is envelope detected. The recorded enveloped wave shape differs from the outgoing acoustic pulse because of the following factors:

(1) impedance mismatch between the seabed and seawater leading to surface scattering of the main pulse;

(1) acoustic instrument parameters such as transmitter power, frequency, pulse length, transducer beampattern, receiver bandwidth and pulse length;

Table 1. Qualitative attributes of reference seabed sites and a four-category classification based on reflectance properties (tail of first echo and energy in second echo)

Site no.	Depth (m)	Sediment type	Substratum appearance in a number of photographic frames or video associated to the echogram	Epibenthic community from the photographs supported by specimens retained in the sled	Viewing of echogram tail first echo	Viewing of echogram second echo	Acoustic seabed classification
a	55	Moderately sorted muddy sand	Flatly sloping	Intermittent low branching sponges/ mollusc beds	Low signal strength, short tail	Low signal strength	Soft-smooth
b	80	Unsorted muddy sand	Flatly sloping, unrippled	Sparse/intermediate irregular, bushy sponges; occasional bioturbation	Low signal strength, short tail	Low signal strength	Soft-smooth
c	34	Unsorted muddy sand	Flat, unrippled with scattered patches of consolidated substratum	Small bushy sponges in clumps	Medium signal strength, long tail	Low–medium signal strength	Soft-rough
d	37	Sorted coarse sand and shell fragments	Flat, regularly rippled (10–30 cm wavelength & amplitude)	Occasional mollusc beds; occasional bioturbation	Medium signal strength, long tail	Low–medium signal strength	Soft-rough
e	80	Unsorted muddy sand	Flatly sloping, unrippled sediment among scattered limestone slabs	Sparse/intermediate irregular, bushy sponges; occasional bioturbation	Low signal strength, short tail	High signal strength	Hard-smooth
f	125	Unsorted muddy sand	Flatly sloping, unrippled sediment adjacent to limestone reef	Occasional irregular bushy and branching sponges; occasional bioturbation	Low signal strength, short tail	High signal strength	Hard-smooth
g	125	Unsorted muddy sand	Flatly sloping, unrippled sediment adjacent to limestone reef	Sparse ascidians/sea pens; evidence of bioturbation	Low signal strength, short tail	High signal strength	Hard-smooth
h	52	Fossiliferous limestone reef	Slabs with crevices and ledges; small (<3 m) pinnacles, walls	Dense gardens of encrusting and erect (cup/finger) sponges, seawhips	Medium–high signal strength, long tail	Medium–high signal strength	Hard-rough
i	115	Fossiliferous limestone reef with layer of sediment	Reef margin: steep (45–90°), high-relief walls (>3 m) with ledges, overhangs, caves, alternating with sloping broken edge and boulders	Dense sponge gardens with occasional large cup sponges, prostrate plate sponges and highly branched finger sponges	Medium–high signal strength, long tail	Medium–high signal strength	Hard-rough
j	125	Fossiliferous limestone reef with layer of sediment	Reef platform: irregular undulations, hummocks; occasional small pinnacles (0.5–1 m) and undercut slabs (~1 sq m)	Intermediate/dense gardens of finger and cup sponges; occasional pancake urchins	Medium–high signal strength, long tail	Medium–high signal strength	Hard-rough

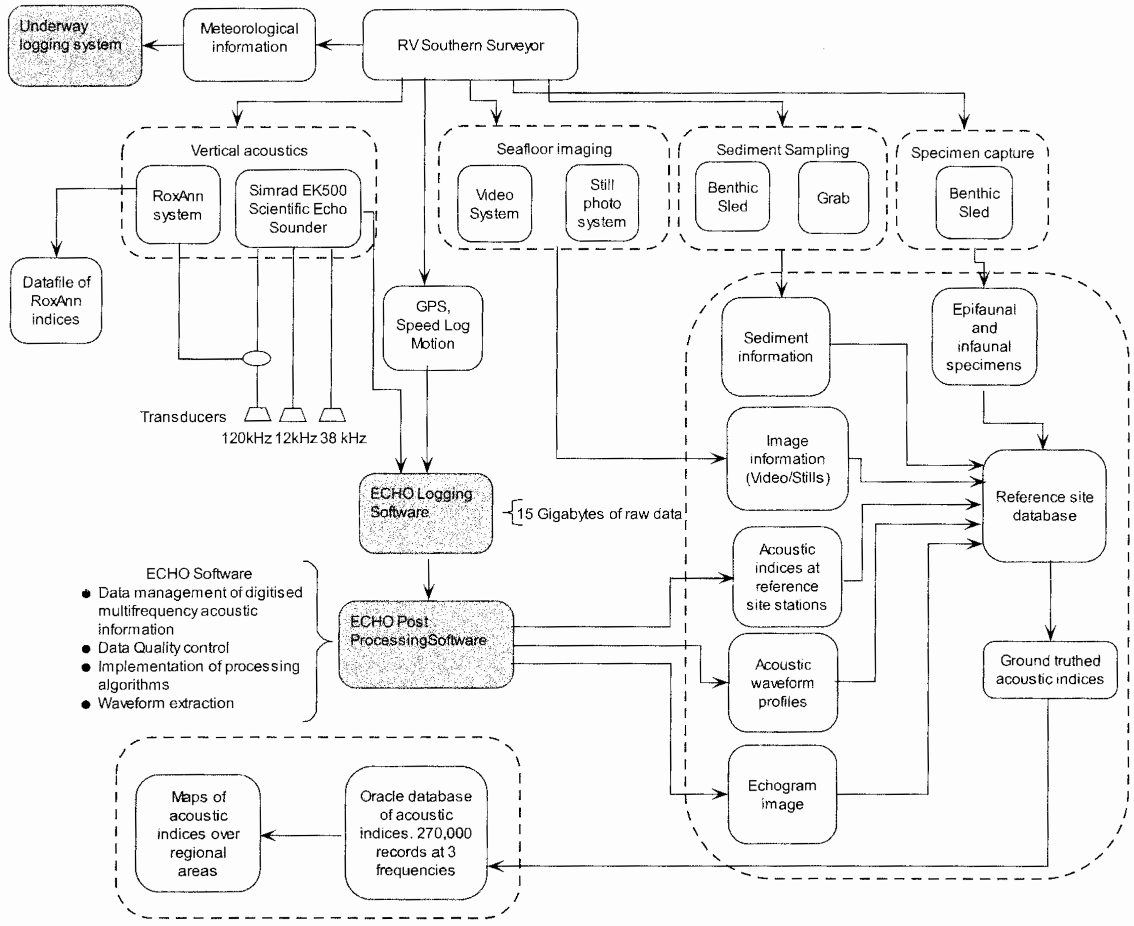


Fig. 2. Flow diagram of the data collection and processing system used to classify seabed types by combining information from acoustic, video, still photographs, sediment and benthic sled samples.

(1) penetration of the acoustic signal into the seabed leading to volume scattering of the main pulse;

(1) directional reflections at the seawater/seabed interface due to seabed roughness;

(1) time delay of off-axis echoes due to spherical spreading with changing depth;

(1) scattering response from the sea surface, vessel hull and subsurface bubbles for the second return echo;

(1) slope of the seabed and stability and trim of the acoustic platform;

(1) attenuation of the signal through the water column; and

(1) acoustic noise on the outgoing and returning signals.

Explicit models that represent the change in acoustic waveform due to this complex scattering and absorption mechanisms in four dimensions do not exist (but see Jackson *et al.* 1986). Simplified models have been developed to extract energy based indices of the seabed in terms of acoustic roughness and hardness (Orlowski 1984; Heald and Pace 1996) and we have used these in the analysis of the collected acoustic data.

Acoustic instrumentation. Acoustic seabed surveys were conducted from the 65 m RV *Southern Surveyor* with a Simrad EK500 echosounder. This echo sounder has a large (160 dB re 1 µPa) instantaneous dynamic range and digitizes the envelope-detected seabed signals from the peak bottom signals (20 dB re 1 µPa) down to sea state or instrument noise (–100 dB re 1 µPa), depending on frequency. The echo sounder was connected to three hull-mounted transducers operating at 12, 38 and 120 kHz. An additional 38 kHz transducer was mounted on a pole that could be lowered 3.5 m below the hull of the vessel in rough weather. The acoustic system was calibrated with a 42 mm tungsten carbide calibration sphere (Foote 1982; SIMRAD software version 5.3). This volume reverberation calibration technique combines the electrical and acoustic constants of the system, G_0^2 (for a given transmitter power, Pt, pulse length, τ, and band width) and the equivalent beamwidth, ψ (provided by the transducer manufacturer). Sound velocity, *c*, and absorption constant, α, are required to give range, *r*, independent values of the volume reverberation signal, Sv dB re 1 µPa at 1m, that is expressed in logarithmic form as:

$$10\log(sv) = 10\log(P_r) + 10\log(r^2 10^{2\alpha r}) - 10\log\left(\frac{P_t G_0^2 r_0^2 \lambda^2 c\tau\psi}{32\pi^2}\right) \quad \text{dB re 1 mPa at 1m.} \qquad (1)$$

The 38 and 120 kHz transducers were split-beam transducers and the 12 kHz transducer was a single beam. One of the beams on the 120 kHz transducer was connected to a RoxAnn seabed instrument set up

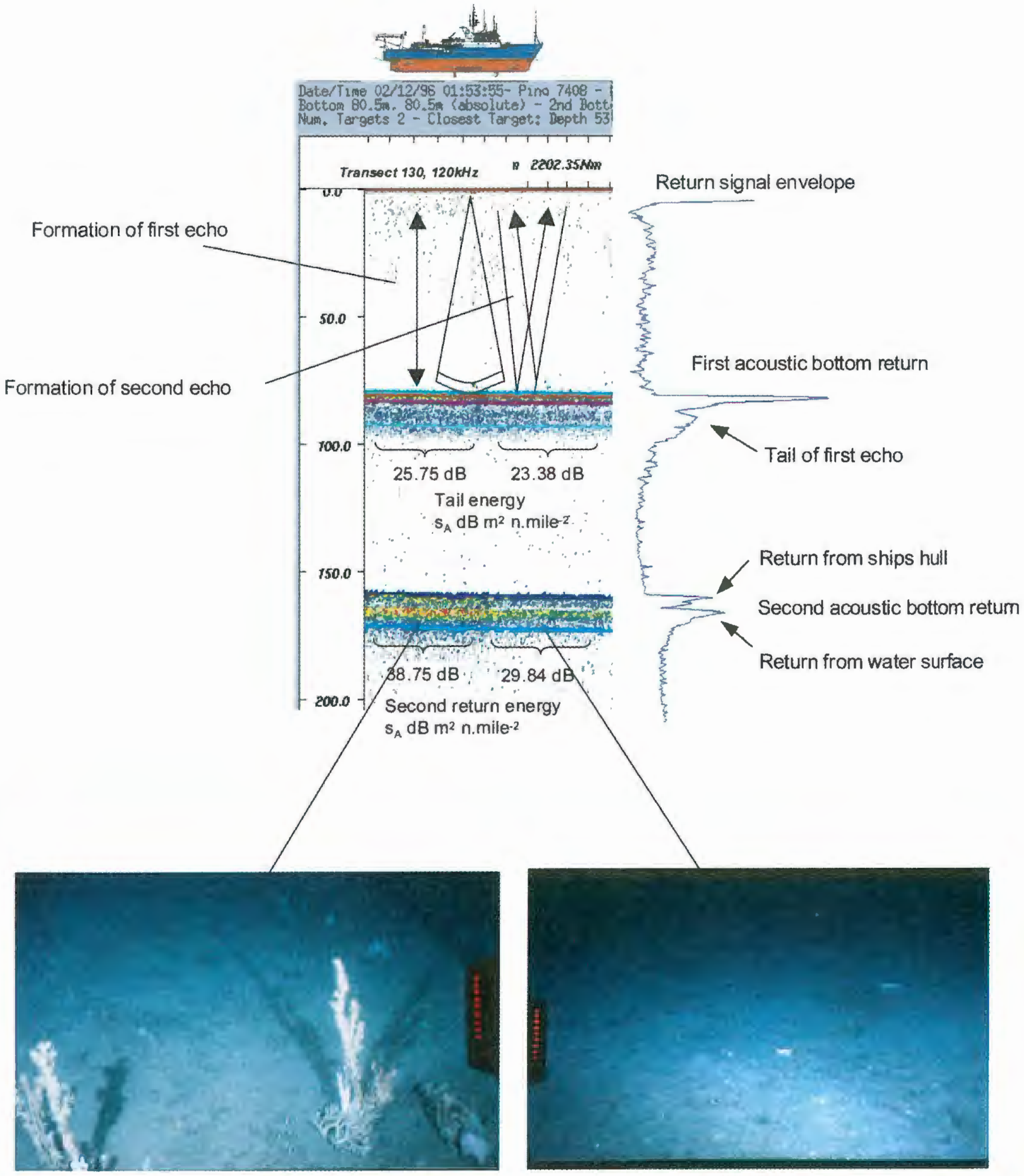


Plate I. Example echogram from the 120 kHz transducer showing the production of the first and second seabed echoes and associated water column scatter as logged by the ECHO software during a benthic sled tow. The echogram and associated still photographs show the transition from hard ground to soft ground and the associated change in benthic fauna. The change in acoustic hardness of the seabed is interpreted from the signal strength of the second echo. The values for acoustic roughness and hardness for the two seabed types are shown in dB.

according to manufacturer's instructions. Details of the acoustic calibration constants for all three transducers are given in Table 2.

Acoustic data collection. Acoustic volume reverberation (Sv) data were logged continuously from three frequencies using a software package, 'ECHO' (Waring *et al.* 1994; Kloser *et al.* 1998). The vessel's pitch/roll (at bottom detection), GPS navigation, speed and the digitized ping Sv dB re 1 μPa data from each frequency were logged. The Sv values from the Simrad EK500 were range-corrected and binned into depth cells. In the May 1996 survey, the three frequencies were digitized in 0.3 m depth cells. This did not provide optimal resolution of the first echo, so in the December 1996 survey the first and second echoes were averaged into either 0.5 m or 1 m bins as well as obtaining high-resolution first bottom echo data in 0.01 m bins. The high resolution first bottom echo was binned at a value greater than twice the pulse length assuring that the Nyquist sampling criterion was

Table 2. Calibration settings for the acoustic instrument

	Frequency			
	12 kHz	38 kHz	120 kHz	38 kHz Pole
Absorption (dB/km)	1	9	43	9
Pulse length (mS)	3	1	1	1
Bandwidth (kHz)	1.2	3.8	1.2	3.8
Calibration constant (Svc)	13.3	27.2	22.7	26.5
Beamwidth (between -3dB points) (degrees)	16/17.5	7.1	11.2	7.3
Equivalent beam width (dB re 1 steradian)	–13	–20.7	–18.5	–20.7

satisfied. Data from the RoxAnn instrument, that summarize limited data energy-based features from many pings, were collected in May 1996 for later comparison with digital data from individual pings. All data were logged on a personal computer integrated with the vessel's GPS. Overall there were 8 weeks of survey time, in which 15 GBytes of acoustic data were collected and archived.

Acoustic data quality (ECHO software). Archived digital bottom data were quality checked by using the ECHO post-processing software to mask out bad data as indicated by obvious signal attenuation, usually because of strong winds and/or sea-state. This signal attenuation could be observed on the echograms by examining the loss of water column acoustic scatter as well as seabed acoustic tail scatter relative to adjacent records. Bad weather produced pronounced aeration under the vessel's hull, resulting in increased acoustic reverberation close to the transducer and a marked attenuation of the tail of the first echo and the whole second echo. When sea conditions were particularly poor, a whole day's data would be lost because of poor acoustic signals. In contrast, the RoxAnn instrument, which was receiving the same poor acoustic signals, continued to classify and record seabed type, with no reference to the low quality of these classifications.

Acoustic data analysis. Simple indices of seabed roughness and hardness were derived from the acoustic data, by integrating the tail of the first echo and all of the first and second seabed echoes (Orlowski 1984; Chivers *et al.*1990; Heald and Pace 1996). The reflected acoustic energy in the tail of the first echo, that is increasingly scattered on a rougher seabed, represents acoustic seabed roughness. Several algorithms were used to implement this in our 'ECHO' software. First, a constant depth algorithm was used to integrate the tail echo from 5 to 20 m below the detected bottom signal. This index was found to increase linearly with depth because of spherical spreading of the beam lengthening the return signal envelopes. To compensate for this lengthening, a second tail echo algorithm was implemented that integrated a constant angular sector of the seabed echo off axis from the normal incident beam (Heald and Pace 1996). The limit on the start angle was based on the pulse length and the minimum water depth. For our depth range and 1 mS pulse lengths, the tail portion of the first echo was integrated between depth intervals, d*i*, as determined by the bottom depth and off-axis angular values, θi, between 20° and 30° referenced to the start of the bottom echo. The pulse length offset was set at 0 and 1.5 m, where:

$$\mathrm{d}i = bottom\_depth * \left(\frac{1}{Cos\theta i} - 1\right) + pulse\_offset.$$

The entire reflected energy in the second echo, that has been reflected from the seabed twice (seabed–ship and sea water surface–seabed–ship), represents acoustic hardness. It was defined as starting at two times the water depth (d1) and ending at two times water depth plus 30 m (d2). Several pings, *p*, were integrated (20–60 depending on vessel speed of 3–10 kn) to reduce between-ping variability in the backscatter returns and to standardize on a unit of length sampled, 92.6 m (0.05 nmile):

$$\bar{S}_A = 10\log_{10}\left(1852^2 4\pi \frac{\sum_{p=1}^{m}\left(\delta d \sum_{d=d1}^{d2} 10^{\frac{sv_{dp}}{10}}\right)}{m}\right) \mathrm{dB\ re\ m^2\ nmile^{-2}} \quad (2)$$

where S_A is the area backscatter coefficient, integrated between the start, *d*1, and stop, *d*2, depth, and δd is the acoustic sampling interval. The derivation of area backscatter stems from fishery acoustic biomass studies and is used here as a relative measure of acoustic energy for volume scattering (SIMRAD 1996).

Reflected acoustic waveforms collected at the 10 reference sites were extracted and compared with physical samples at various depths. In order to compare the echo tail energy and shape at different depths, the signals were transformed to a reference depth of 100 m. The tail echos (defined as commencing after a delay of the pulse length in water) were resampled at an effective rate of the ratio of the water depth to the reference depth.

Results

RoxAnn acoustic analysis

Acoustic seabed classifications obtained with the RoxAnn system on the 120 kHz transducer contained major depth biases (Fig. 3). The depth bias in these data (393407 points collected over a four-week survey) could not be explained by differences in bottom type as determined from sediment and photographic samples. Both the roughness and hardness indices reached a maximum and were then clipped at 130 and 70 m, respectively. The depth trend prior to data clipping could be removed by carefully extracting data from calm days, and the resulting data compared favourably with data from our own algorithms, and field-based sampling with photographic, video and sediment samples. Data beyond 70 m for the hardness parameter could not be recovered and we discontinued use of the data set.

Digital acoustic data analysis

The digital data were calibrated, quality assured and processed as outlined in the methods, with scatter plots of the indices produced to observe trends with depth and frequency. The 120 kHz frequency data appeared to need no overall depth correction for any of the extracted indices. A slight trend in the constant angle algorithm was observed in shallow water, <50 m. This was caused by an error in our

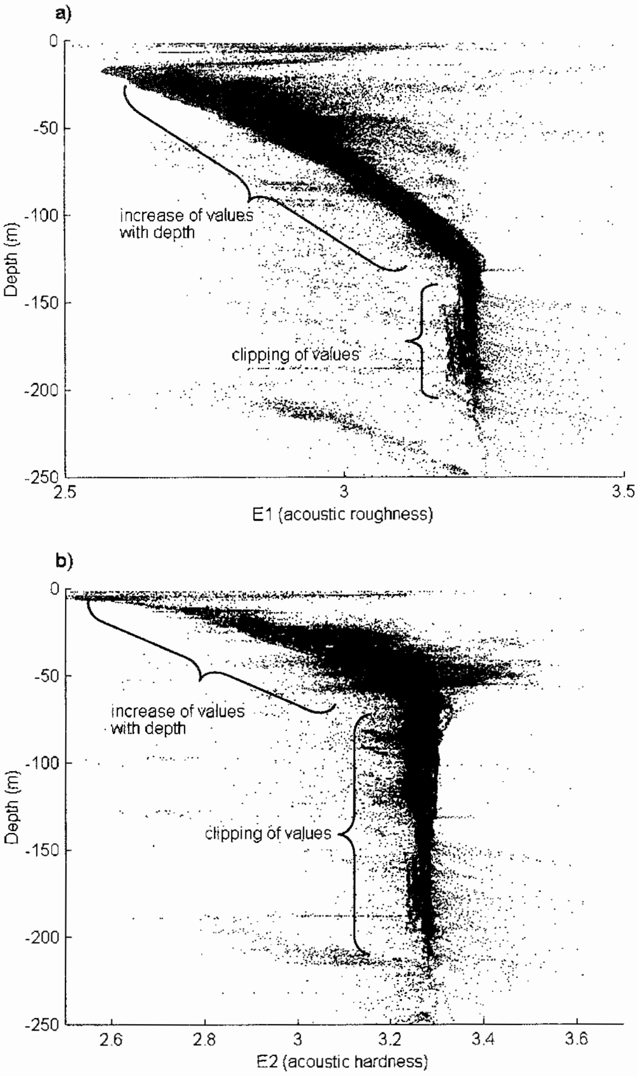


Fig. 3. Scatter plot of RoxAnn indices, E1 (roughness) and E2 (hardness), with depth collected during a four-week voyage. The indices show a clear depth bias and once clipped could not be recovered. Use of these data was discontinued due to this bias and uncertain data quality.

algorithm and was corrected by introducing a pulse offset of 1.5 m. A much greater depth bias occurred with the 38kHz data, Fig. 4(*a*), which was also corrected by introducing a pulse offset of 1.5 m. Figure 4(*b*) shows the uncorrected energy of the first echo tail that required a linear correction of –0.08 dB m^{-1}, Fig. 4(*d*). The total second echo energy for the 38 kHz frequency needed no obvious depth correction, Fig. 4(*c*).

Surficial sediment data

Mean sediment grain size is plotted against the derived acoustic indices and depth for one frequency 120 kHz (Fig. 5 *a*–*c*). There is a slight correlation between the hardness and roughness parameters and phi size (Figs 5*b* and 5*c*). This correlation occurred for all frequencies —12, 38 and 120 kHz — with r^2 of 0.3, 0.3 and 0.5 for acoustic hardness and 0.1, 0.2 and 0.3 for acoustic roughness, respectively. The plot of the residuals shows a random relationship for all frequencies and both indices. We did not observe a depth-related bias in the sediment size for depths less than 170 m, Fig. 5*a* (r^2 = 0.03) and there was no trend in the residuals that we could ascertain from the data collected. Sediment samples at depths greater than 170 m were not included in the linear model as they appear to contain larger grain sizes when compared with previous studies (Bax and Williams 2000). This suggests that some winnowing may have occurred in our sediment samples from greater depths.

Reference sites

The 10 reference sites were characterized by depth, sediment type, substratum appearance and epibenthic community (Table 1). Based on the characteristics of the first and second echoes, the 10 sites were divided into 4 seabed types: soft-smooth; soft-rough; hard-smooth; and hard-rough. Acoustic hardness and roughness indices for both the 38 and 120 kHz were plotted against these seabed types.

There is general agreement between seabed types, confirmed with physical and photographic sampling, and the acoustic roughness and acoustic hardness indices (Fig. 6). There are obvious outliers, for both soft-rough (reference Site *d*; Plate II*d*) and hard-rough (reference Site *h*; Plate II*h*) seabed types. Photographs show that these stations represent the extreme of our simple classification system. Reference Site *d* was a coarse sand sediment (phi 0.2), with large (10–30 cm) wavelength and large (10–30 cm) amplitude sand/shell regular wave patterns (Plate II*d*). The acoustic indices for this seabed were hard because of the coarse sediment and shell debris and very rough because of the sand waves.

The difficulty in characterizing the soft-rough seabed feature is highlighted by observing the average first echo tail waveforms of the four different seabed types referenced to 100 m at 38 and 120 kHz (Fig. 7*a* and *b*). The soft-rough seabed type is distinct at 38 kHz, but merges with the hard-smooth seabed type at 120 kHz, showing the dependence of seabed classification on acoustic frequency.

Reference site *h* (Plate II*h*) was a very rough hard reef with large boulders of 2–3 m vertical extent and massive branching epibenthos that represents the extreme of the rough-hard seabed types. There was a marked difference in the roughness index for this site for the two frequencies, which again highlights the frequency dependence of seabed typing by using acoustic systems.

Discussion

One of the important observations that has come from this work is the difficulty of remote sampling the seabed for biological and geological information in the open ocean.

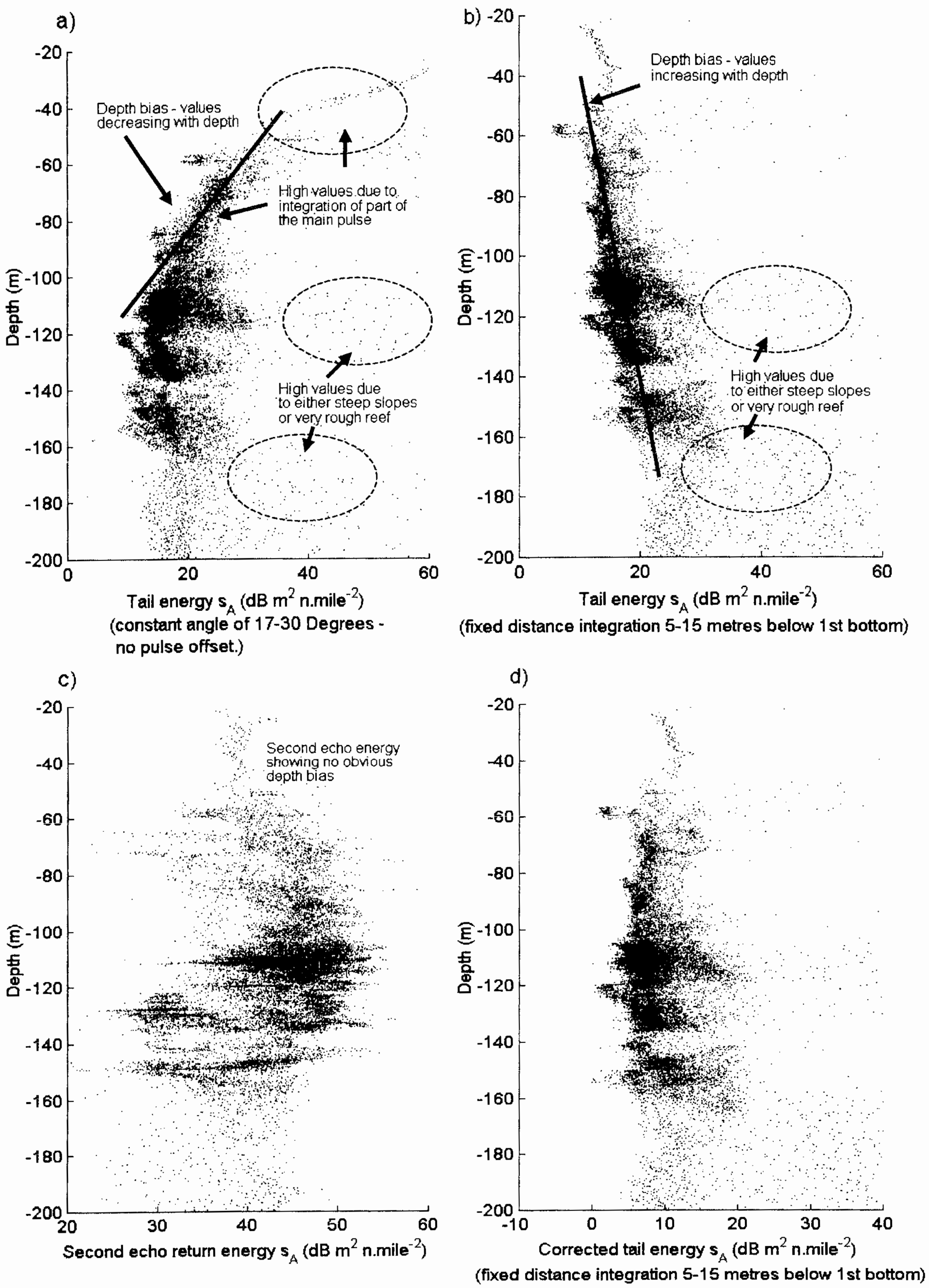


Fig. 4. Scatter plot of 40000 uncorrected acoustic indices: *(a)* tail of first echo constant depth, 38 kHz with depth bias at shallow depths due to integration close to the high-energy surface scattered echo; *(b)* tail of first echo constant angle, with depth bias due to time spreading, 38 kHz; *(c)* energy of second echo with no obvious depth bias, 38 kHz; and *(d)* tail of first echo, 38 kHz with depth bias removed.

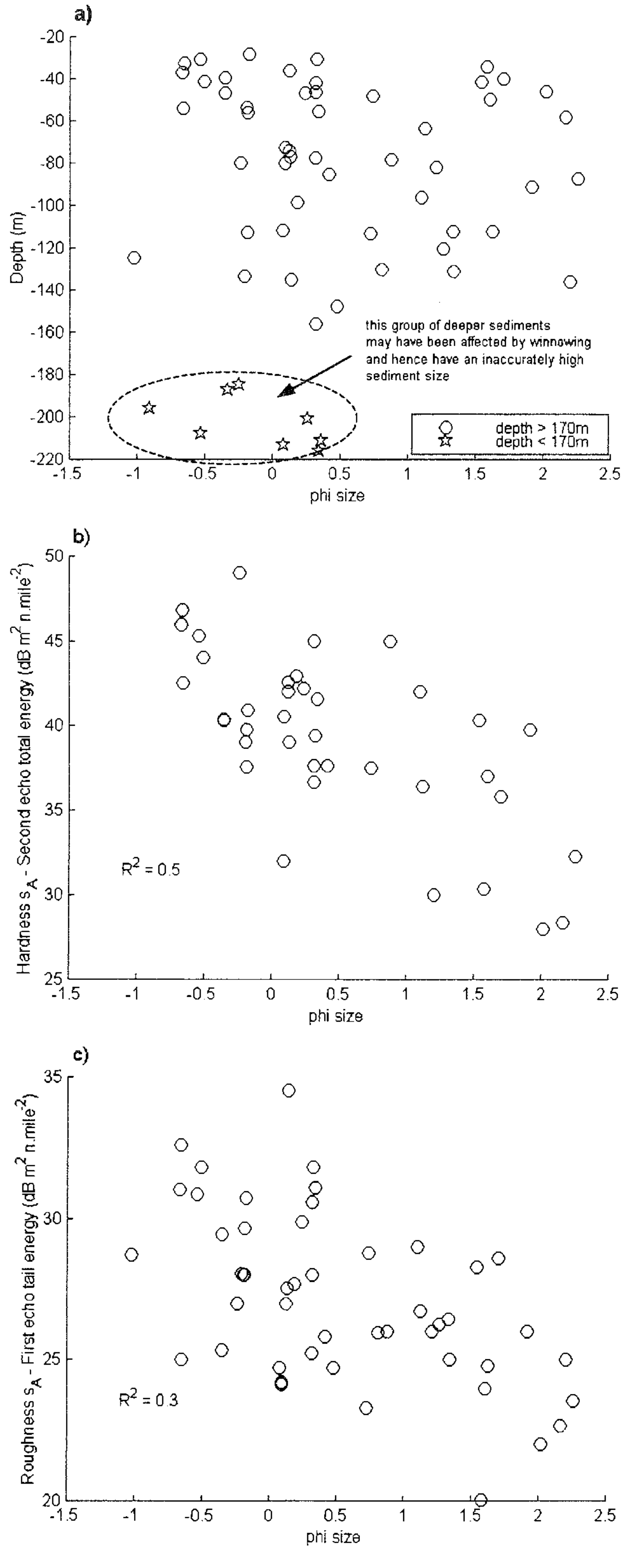


Fig. 5. Scatter plot of mean sediment phi size against depth, acoustic hardness, acoustic roughness and associated goodness-of-fit to a linear model. Samples collected from deeper than 170 m have been removed because of suspected winnowing of smaller sediments.

This was due to the various sea states we encountered, which at times reached 40–50 knot winds and 4–5 m seas. Maintaining data quality of our hull-mounted acoustic system was difficult and required that we log the digital data and use rigorous post-survey quality control. The ECHO software was used to exclude regions of bad data from the analysis (Kloser *et al.*1998). This interactive software enables the user to make changes in colour map, dynamic range, calibration, noise and bottom algorithms. The results of changes can then be directly observed in a 'what you see is what you get' (wysiwyg) software environment. This level of quality control resulted in rejecting entire days of data collected on particularly rough days. In contrast, the commercial instrument operating at the same time continued to classify and record seabed types with no notation that the data were of very poor quality and classifications were based primarily on acoustic interference.

Overall, our use of the commercial seabed system did not yield repeatable results and could not be used at depths greater than 70 m. Such devices cannot be relied on for repeatable measurements in the variety of sea and background noise conditions that we operate under. Others have experienced problems with this system and advocate the use of constant speed because of sensitivities to noise and/or subsurface bubbles (Hamilton *et al.* 1999). On the other hand, other researchers have obtained good results with the instrument (Magorrian *et al.* 1995; Greenstreet *et al.* 1997), although biases due to depth or ship speed were noted by both researchers.

A second major advantage of archiving calibrated digitized waveforms for subsequent quality control (instead of summary descriptors) is that the original data are available for subsequent analyses. Seabed typing is in its infancy and will only proceed through exploratory analyses of calibrated digital data collected from well described reference sites. We are now at the stage where we can introduce new algorithms (energy and shape based) that can describe more of the variability in seabed type than the simpler indices available at present. These can then be tested against our present reference sites and against future reference sites in different regions or collected from different platforms because all acoustic data are calibrated and digitized.

An alternative platform for acoustic sampling is the commercial fishing vessels. Fishers make extensive use of echo-sounders for targeting seabed type based on their interpretation of the acoustic returns and deployment (successful or not) of fishing gears (Bax and Williams 2001). Their interpretation of echo sounding is similar to the quantitative energy descriptors described by Orlowski (1984) and Heald and Pace (1996), and this raises the possibility that echo-sounders on fishers' vessels could be used to collect acoustic data and map the seabed during their routine operations. If we could calibrate and record acoustic

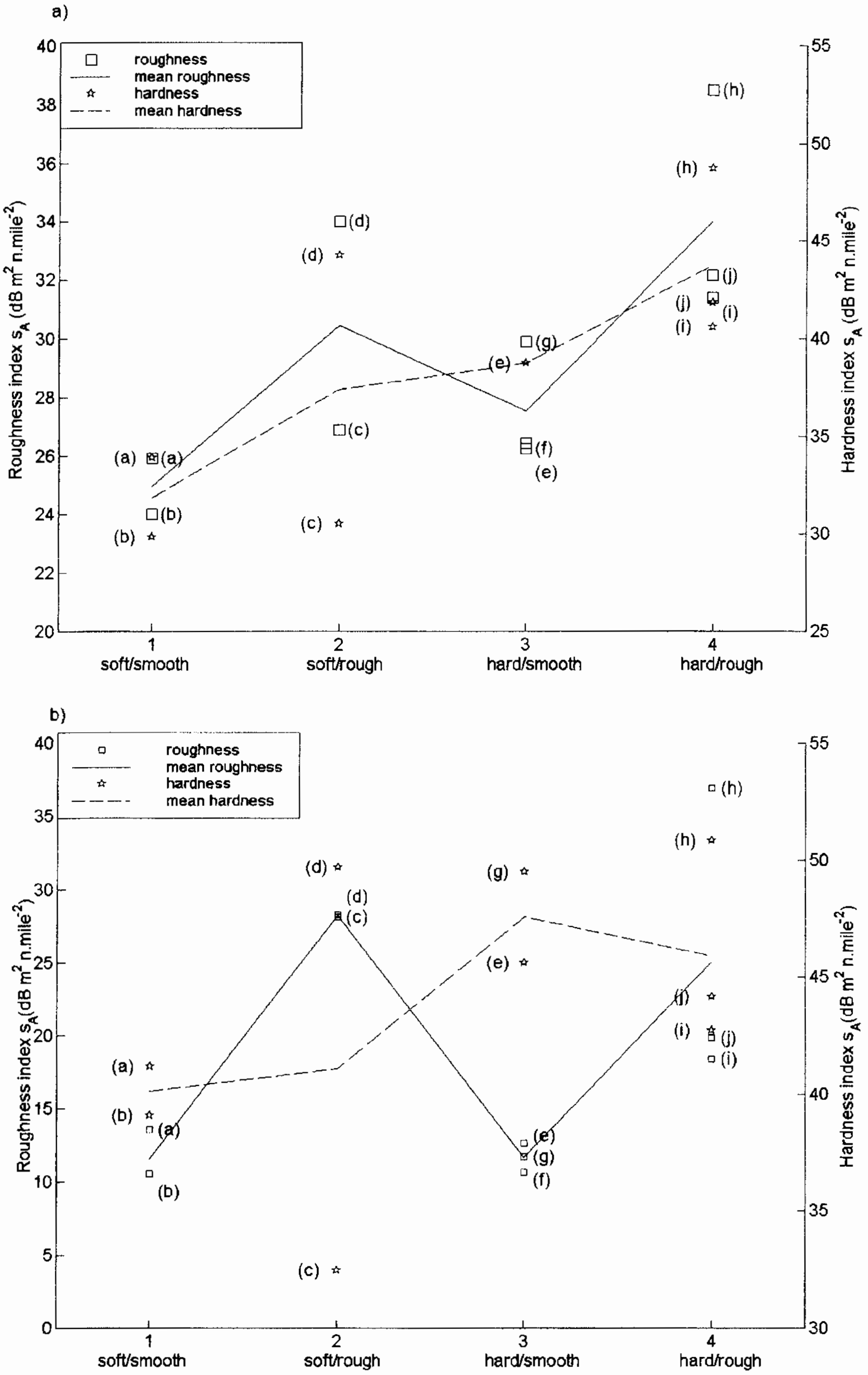


Fig. 6. Scatter plot and means for hardness and roughness acoustic indices associated with seabed types of soft-smooth, soft-rough, hard-smooth and hard-rough for two frequencies, *(a)* 120 kHz and *(b)* 38 kHz. The reference sites were at depths ranging from 33 to 230 m.

data collected by the fishing industry it would enable large areas of the shelf seabed to be mapped, without the high costs of a dedicated survey.

One of the issues that we foresaw in using acoustics over a relatively large depth range (30–230 m) was a depth bias. A depth-related bias occurs (at least in part) due to the greater sampling area with increasing depth because of spherical spreading of the beam. The physical mechanism for this process has been described and corrections attempted. In particular, Orlowski (1984) measured a depth


(a) Soft/Smooth
55 m


(b) Soft/Smooth
80 m

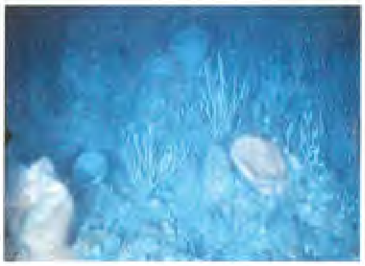

(c) Soft/Rough
34 m


(d) Soft/Rough
37 m


(e) Hard/Smooth
80 m


(f) Hard/Smooth
120 m


(g) Hard/Smooth
120 m


(h)Hard/Rough
55 m


(i) Hard/Rough
120 m


(j) Hard/Rough
120 m

Plate II. Seabed images from the 10 reference sites *a–j* corresponding to the classifier descriptions outlined in Table 2. (Tow bridle of camera platform visible in most photographs.)

dependency when studying the reflection from the first and second seabed echoes, finding the results from depths less than 50 m to be unexplainable. From our scatter plots (Fig. 4) of the acoustic indices we did not appear to have an obvious depth-related bias for the acoustic roughness and hardness parameters. The constant depth roughness algorithm does have a depth bias for 38 kHz, but after linear model correction, compares well with the constant angle algorithm for the latter part of the depth range. The 120 kHz system did not appear to have a depth-related bias perhaps because of the wider beam width (10°) of this transducer. This result suggests that a wider beam width system is more

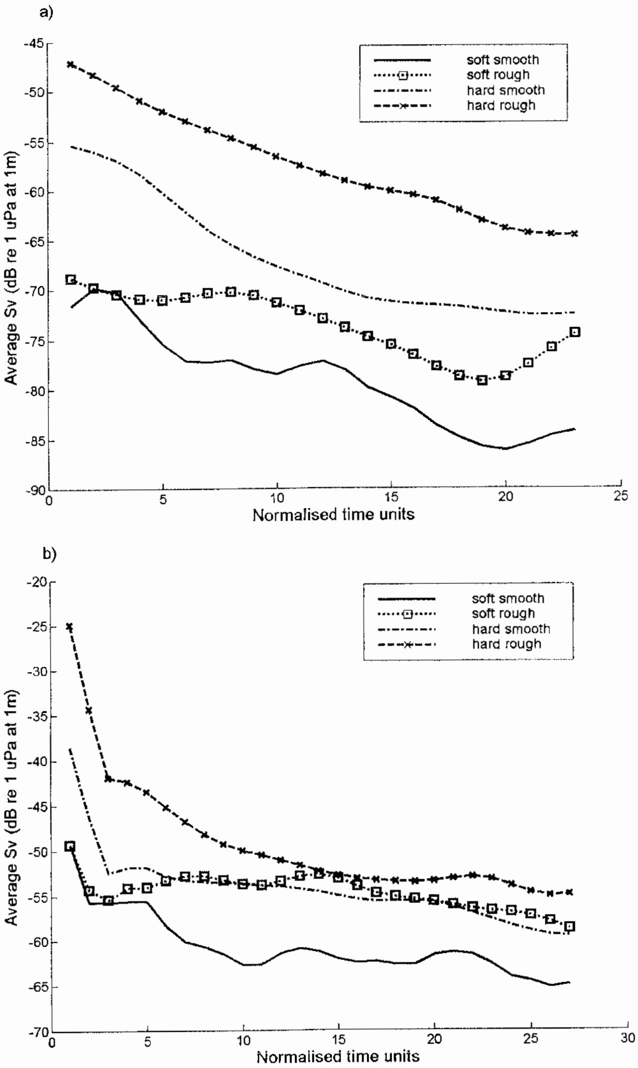


Fig. 7. Waveforms of the averaged seabed echoes for reference habitat types of soft-smooth, soft-rough, hard-smooth and hard-rough after compensation for depth at *(a)* 38 kHz and *(b)* 120 kHz.

suitable for obtaining these types of bottom roughness scatter measurements. This is consistent with improved discrimination of bottom scattering strength as a function of sediment size with increased angles of incidence (Urick 1983, p. 277).

Slope of the seabed introduced a bias that was difficult to exclude without a knowledge of the underlying bathymetry. Steep slopes produced large acoustic roughness values and low acoustic hardness values. If the vessel was transecting normal to the slope, these values could be flagged, but if the vessel was steaming parallel to the slope contours the values could only be interpreted once the data were plotted on a bathymetric map of the region. On very steep slopes such as drop offs from reefs, the large roughness parameter is indicative of a unique biological community and would be important to leave in the data set. This type of information could be excluded in data cleaning procedures used currently for the RoxAnn system (Greenstreet *et al.* 1997; Hamilton *et al.* 1999). Hence a seabed that produced a very high acoustic roughness and a very low acoustic hardness was indicative of sloping ground. The narrow-beam 38 kHz transducer seemed to be more sensitive to seabed slope than the wider beam 120 kHz system.

One of the tests for the acoustic hardness index was its ability to discriminate sediment grain size over a range of depths. Although the relationship is relatively weak — grain size explained 50% of variability in the hardness index for the 120 kHz system — it is a surprisingly good result given the simplicity of this acoustic index that measures only the total acoustic backscattering energy in the second bottom echo. The theory of the scattering mechanisms that make up the second echo is poorly understood (but see Heald and Pace 1996) and the effect that changing surface roughness, subsurface aeration (wind or propeller cavitation) and different hull shapes has not been quantified. Similarly, the backscatter from the same hull shape for changing pitch and roll angles is also open to question. Finally, sediment size is only one of many factors that constitute acoustic backscattering; sediment porosity, bulk density and surface roughness are also major contributors (Urick 1983).

The suitability of the second echo as a proxy for sediment size, or more correctly sediment hardness, is a significant step. Physical sediment surveys are expensive and consequently either cover a small area or a larger area at low resolution. Sediment sampling on the south-east Australian shelf has been performed by very sparse sampling with transects spaced every 20 Nm and stations every 10 nmile across the shelf (Davies 1979; Jones and Davies 1983). With acoustic methods, we are observing inferred changes in sediment properties at the scale of 0.5 nmile during continuous steaming at 8 kn or more, depending on sea state. However, acoustic sampling itself is at present insufficient to describe sediment properties without concomitant ground-truthing. Combining surficial sediment sampling with the acoustic hardness index provides a realistic option to improve the sediment maps of this region (Plate III*b*).

The reference seabed set established for ground-truthing in this study incorporated acoustic, video, photographic and benthic sampling. Our simple description of four seabed types based on a combination of biological and geological attributes is evolutionary (Bax *et al.* 1999). Therefore, we were encouraged by the consistency across depths for the soft-smooth, hard-smooth and hard-rough seabed types and their correct acoustic classification. Of interest was the anomalous soft-rough classification, where sand waves of coarse grain were classified as hard-rough by using the simple acoustic indices. There can obviously be a mismatch between acoustic-determined seabed types determined from

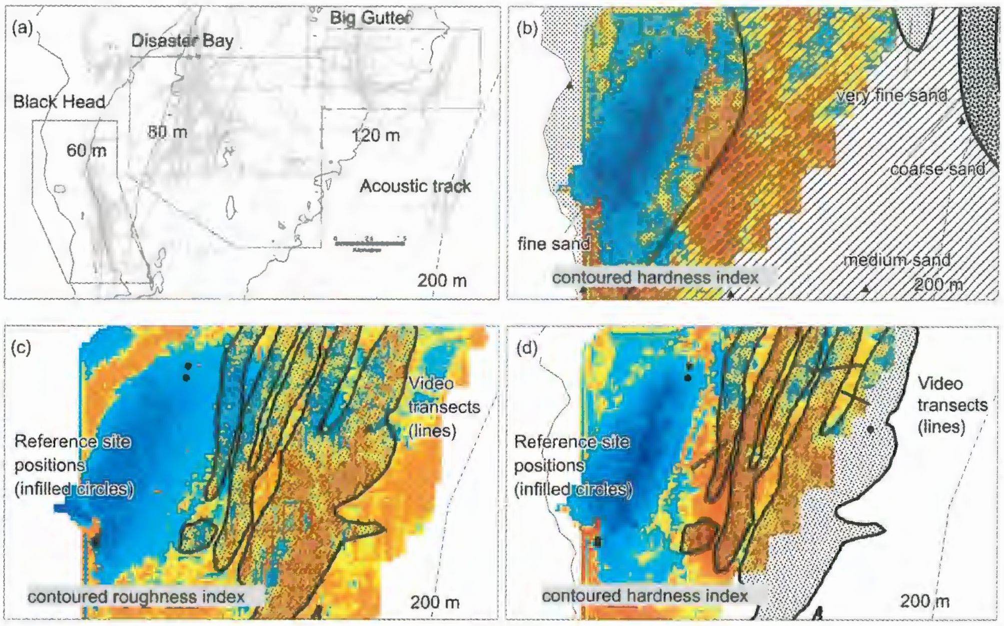


Plate III. Maps of acoustic hardness and roughness indices (120 kHz) compared with other maps of the region: *(a)* bathymetry with acoustic transects and habitat regions overlaid; *(b)* acoustic hardness with sediment maps from Davies (1979); *(c)* acoustic roughness with fishers' map of untrawlable ground map (Bax and Williams 2001); and *(d)* acoustic hardness with fishers' map of untrawlable ground map. Blue represents a low index value and orange a high value. Video transects used to study fine scale differences in the fishers' and acoustic maps are highlighted with dark lines.

these simple acoustic indices and seabed types determined from physical sampling and *in situ* visual examination. The importance of *in situ* visual examination as well as sediment sampling is suggested by the Greenstreet *et al.* (1997) review of RoxAnn. These authors found that six or seven seabed types were distinguished acoustically, but sediment sampling could confirm only three types. Sediment sampling would not have picked up features such as sand waves and it remains unclear whether the RoxAnn or the physical sediment samples provide a more realistic representation of the seabed in their area.

To compare our maps with those of previous studies on seabed character in this region we mapped the acoustic indices for the intensely sampled meso-habitats (Big Gutter, Disaster Bay and Black Head), using Vertical Mapper in Mapinfo (rectangular interpolation, cell size 0.005 deg., search radius 0.01 deg.). These maps are overlaid with bathymetry (Plate III*a*), and fishers' interpretation of seabed type (Plate III*c* and *d*). There is general agreement between the maps at large scale >10 km but not at fine scale <1 km (Williams and Bax 2001). The fine scale resolution of the acoustic maps highlights differences in interpretation between acoustic maps and fishers' maps at this single frequency. Detailed video sampling stations (159, 190 and 195, Plate III*c* and *d*) at transition points in these maps support the acoustic interpretation of acoustic hardness and roughness for biological and seabed attributes as defined in our reference set (Table 2), suggesting that the fishers' seabed classification scheme is not consistent with our own. This is perhaps not surprising given that the two classification schemes have been developed for different purposes.

In this study we collected information from three frequencies, each of which has proven useful for seabed classification purposes. The 120 kHz, wavelength 1.25 cm system proved to be the most sensitive to noise because of the large absorption of the signal with depth. It provided the best visual discrimination in shallow water and this may be due to its wider beamwidth (Bax *et al.* 1999). It also seemed the most responsive to sediment size with a correlation coefficient of 0.5. The 38 kHz, wavelength 3.95 cm, system was the best mid-depth system (100–250 m), as the noise of the vessel did not effect the second echo. In rough weather we were able to lower a 38 kHz transducer 3.5 m below the hull and greatly reduce surface bubble attenuation problems. Hence, this system could operate in far more severe weather conditions. The usefulness of the 12 kHz system was not fully explored in this analysis because of its poor discrimination of surficial sediment data.

Combined use of all three frequencies for classification of seabed types is part of ongoing research. Initial results of combining all three frequencies with energy and shape based features of the echo show great promise (Kavli *et al.* 1994; Kloser *et al.* 1998; Pitcher *et al.* 1999). The promise of multifrequency techniques is suggested by the large variability in the simple roughness and hardness indices observed with the 38 and 120 kHz frequencies, implying that the different frequencies (or potentially different beam widths) obtained different information (or the same information at different scales) from seabed features. More detailed classification and signal extraction methods on a larger number of frequencies may be able to classify a larger number of seabed types with greater consistency. However, we stress again that this will only be possible by using calibrated acoustic data in their raw form, collected from reference areas that have been ground-truthed.

Looking to the future, we will expand our limited reference set to form a comprehensive reference set of seabed descriptors. To date, we have used only simple, vertical single-beam acoustic systems. However, the advantage of the methodology described here is that it can be applied to calibrated acoustic data collected from a broad range of sampling platforms from fishing vessels to multi-frequency, split beam scientific sounders or even higher resolution swath mapping acoustic systems such as digital sidescan sonars and multibeam echo sounders. This will enable more detailed and more consistent seabed classifications to be made in the future to assist the mapping, management and monitoring of the Australian Marine Jurisdiction.

Acknowledgments

This research was funded by grants number T93/237 and 94/040 from the Fisheries Research and Development Corporation (FRDC). Dr Andrew Forbes and Dr Alan Butler are thanked for review of the manuscript as well as two external reviewers. Our reviewers reminded us that the RoxAnn system and in particular Dr D. Burns has made a valuable contribution to the topic of seabed mapping. We acknowledge this and reinforce it here but point out that users should be cautious when using black box implementations of acoustic backscatter systems without viewing the raw data. Matt Sherlock, Lindsay MacDonald and Jeff Cordell are thanked for assistance in collection of acoustic data at sea. Dr Pavel Sakov and Jason Waring are thanked for the ECHO software developments and assistance in algorithm developments.

References

Barker, B. A. J., Helmond, I., Bax, N. J., Williams, A., Davenport, S., and Wadley, V. A. (1999). A vessel-towed camera platform for surveying seafloor habitats of the continental shelf. *Continental Shelf Research* **19**, 1161–70.

Bax, N., Kloser, R. J., Williams, A., Gowlett-Holmes, K., and Ryan, T. (1999). Seafloor habitat definition for spatial management in fisheries: a case study on the continental shelf of southeast Australia using acoustics and biotic assemblages. *Oceanologica Acta* **22**(6), 705–19.

Bax, N. J., and Williams, A. (Eds.) (2000). Habitat and fisheries productivity in the South East Fishery. Final report to FRDC Project 94/040. (CSIRO Marine Research: Hobart, Australia.)

Bax, N. J., and Williams, A. (2001). Seabed habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring. *Marine and Freshwater Research* **52**, 491–512.

Chivers, R. C., Emerson, N., and Burns, D. R. (1990). New acoustic processing for underway surveying. *Hydrographic Journal* **56**, 9–17.

Coleman, N., Gason, A. S. H., and Poore, G. C. B. (1997). High species richness in the shallow marine waters of south-east Australia. *Marine Ecology Progress Series* **154**, 17–26.

Collins, W., Gregory, R., and Anderson, J. (1996). A digital approach to seabed classification. Sea Tech, August 83–7. ISSN 0093-3561.

Folk, R. L. (1968). 'Petrology of Sedimentary Rocks.' (Hemphill: Austin, TX.)

Foote, K. G. (1982). Optimizing copper spheres for precision calibration of hydroacoustic equipment. *Journal of the Acoustical Society of America* **71**, 742–7.

Greenstreet S. P. R., Tuck I. D., Grewar G. N., Armstrong E., Reid D. G., and Wright P. J. (1997). An assessment of the acoustic survey technique, RoxAnn, as a means of mapping seabed habitat. *ICES Journal of Marine Science* **54**, 939–59.

Hamilton, L. J., Mulhearn, P. J., and Poeckert, R. (1999). ComparisonHamilton, L. J., Mulhearn, P. J., and Poeckert, R. (1999). Comparison of RoxAnn and QTC-View acoustic bottom classification system performance for the Cairns area, Great Barrier Reef, Australia. *Continental Shelf Research* **19**, 1577–97.

Heald, G. J., and Pace, N. G. (1996). An analysis of the 1st and 2nd backscatter for seabed classification. In 'Proceedings of the 3rd European Conference on Underwater Acoustics, 24–28 June 1996'. Vol. II. (Ed. J. S. Papadakis.) pp. 649–54. (Crete University Press.)

Jackson, D. R., Winebrenner, D. P., and Ishimaru, A. (1986). Application of the composite roughness model to high-frequency bottom scattering. *Journal of the Acoustical Society of America* **79**(5), 1410–22.

Jones, H. A., and Davies, P. J. (1983). Superficial sediments of the Tasmanian continental shelf and part of Bass Strait. Bureau of Mineral Resources, Geology and Geophysics Bulletin No. 218. (Australian Government Publishing Service.) ISBN 0 644 02686 3. 25 pp.

Kaiser, M. J.; Armstrong, P. J.; Dare, P. J., and Flatt, R. P. (1998). Benthic communities associated with a heavily fished scallop ground in the English Channel. *Journal of the Marine Biological Society* **78**(4), 1045–59

Kavli, T., Weyer, E., and Carlin, M. (1994). Real time seabed classification using multi frequency echo sounders. In 'Proceedings of Oceanology International 94, Brighton, UK, March 1994'. Vol. 4, 1–9.

Kloser, R. J., Sakov, P. V., Waring, J. R., Ryan, T. E., and Gordon, S. R. (1998). Development of software for use in multi-frequency acoustic biomass assessments and ecological studies. CSIRO Report to Fisheries Research and Development Corporation T93/237: 74 pp. (CSIRO Marine Research: Hobart, Australia.) ISBN 0 643 06192.4.

Lurton, X., and Pouliquen, E. (1992). Automated seabed classification system for echo-sounders. In 'Oceans 92, Vol. 1'. pp. 317–21. (IEEE: New York.)

Magorrian, B. H., Service, M., and Clarke, W. (1995). An acoustic bottom classification survey of Strangford Lough, Northern Ireland. *Journal of the Marine Biological Association United Kingdom* **75**, 987–92.

Orlowski, A. (1984). Application of multiple echoes energy measurements for evaluation of sea-bed type. *Oceanologia* **19**, 61–78.

Pitcher C. R., Gordon, S. R., Kloser, R. J., and Jones, P. N. (1999). Development of an acoustic system for remote sensing of benthic fisheries habitat for mapping, monitoring and impact assessment. CSIRO Report to Fisheries Research and Development Corporation T93/237: 74 pp. (CSIRO Marine Research: Hobart, Australia.) ISBN 0 643 06196 7.

SIMRAD (1996). Simrad EK500 Scientific Echo Sounder Instruction Manual. Simrad Subsea P2170E. 111 pp. (Simrad: Horton, Norway.)

Snelgrove, P. V. R., and Butman, C. A. (1994). Animal–sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology: an Annual Review* **32**, 111–7.

Urick, R. J. (1983). 'Principles of Underwater Sound.' (McGraw-Hill: New York.) 423 pp.

Waring J. R., Kloser R. J., and Pauly, T. (1994). 'Echo' – managing fisheries acoustic data. In 'Proceedings of the International Conference on Underwater Acoustics. University of New South Wales, December 1994'. pp. 22–4. (Australian Acoustical Society: Darlinghurst Public School, NSW, Australia.)

Manuscript received 10 December 1999; revised and accepted 28 August 2000

Mar. Freshwater Res., 2001, **52**, 491–512

Seabed habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring

Nicholas J. Bax and Alan Williams

CSIRO Marine Research, Hobart, Tas. 7001, Australia

Abstract. A hierarchical approach to mapping seabed habitat is presented. A provincial scale survey that included hydrography and geology provided the context for interpreting habitat use and vulnerability. A megascale map, developed in cooperation with local fishers, identified major seabed features (kilometres to 10s of kilometres). Vulnerability of a feature was defined as its resistance to physical modification and its resilience, or capacity to recover, on removal of the modifier. Vulnerability was assessed from geological, biological and oceanological properties. Inner-shelf sandstone and limestone reefs that were exposed and weathered during the last ice age, and shelf-break bryozoan patch reefs, appear to be the most vulnerable of the hard-grounds to physical disturbance. In contrast, larger, high-relief, outer-shelf fossiliferous limestone reefs appear relatively invulnerable to physical disturbance from fishing. Megascale features were the focus of detailed physical and biological sampling at the mesoscale level (10 m to km), the level of resolution necessary for establishing baseline conditions and monitoring change. The hierarchical approach used here to map seabed habitat amalgamates scientific and fishers' information. Approached in this way, habitat mapping has the potential to build a common framework of knowledge on which effective spatial management can be based.

Introduction

The greatest fishing effort within the South East Fishery (SEF) occurs on the continental shelf off south-eastern Australia. Trawling started in the early 1900s, and today a large fleet is made up of five sectors: otter-trawlers, Danish seiners, demersal longline and dropliners, gillnetters and trappers (Tilzey 1999; Klaer 2001). Effort in the fishery continues to rise, despite recent management attempts to reduce it (Larcombe *et al.* 2001). Several of the economically important species are targeted by two, three and in one case four sectors, often in similar or adjacent habitats. Adoption of advanced navigational aids (track plotters and GPS) and gears that fish rough-ground effectively, has enabled effort in all sectors to be increasingly targeted at the 'hard-ground' habitat features that attract fish (Bax and Williams 2000). This has increased fishers' awareness of the importance of particular habitats and changes that occur. Some fishers report substantial erosion and disappearance of seafloor features in recent years as a result of increased targeted effort; others suggest that natural movement of sediments is covering individual reefs.

The dependence of fish community structure on local seafloor features was one of the ecosystem attributes considered to have high leverage for management intervention (*sensu* Senge 1990), in a 5-year study of the south-eastern Australian continental shelf ecosystem (Bax *et al.* 1999; Bax and Williams 2000). The functional value of seafloor features and their potential to be modified by fishing (and other) practices indicated that management to conserve critical seafloor features would contribute to the long-term sustainability of the fishery ecosystem. This led to an extensive program of seabed mapping, the primary objective of which was to provide scientific advice to resource managers that could be used to improve long-term sustainable management of local fisheries, the supporting ecosystem and attendant biological diversity.

The continental shelf that we see (or remotely sense) today is the product of complex interactions between marine and terrestrial processes superimposed on tectonic processes that stretch back hundreds of millions of years (Bernecker *et al.* 1997). The southernmost extension of the Bega Batholith, a granite intruded in the Devonian, ~345–395 million years ago, is across the continental shelf of eastern Victoria. These Devonian granitic rocks appear today as distinctive jointed rocky outcrops such as the New Zealand Star Banks, a noted shipping hazard. Continental shelf sediments in the study area derive from terrestrial and biological origins. Bryozoan sands dominate on the outer shelf and are a mix of modern and relict sediments from the Quaternary and Tertiary (0–2 million and 2–65 million years ago, respectively; Wass *et al.* 1970). The modern bryozoan content of sands ranges from 5% to 85%, but generally accounts for 20–50%. They are dominated by reteporiform Zoaria, suggesting that they were produced in a relatively low energy environment (Wass *et al.* 1970). Short

10.1071/MF00003 1323-1650/01/040491

term (~10^5 years) sea level changes associated with glacial advances and retreats in the Pleistocene have influenced the deposition and reworking of sediments (Fleming and Roberts 1973; McLean *et al.* 1978). During the most recent Ice Age, 10 000 to 2 million years ago, when sea levels were at least 100 m lower than present, currently submerged inner shelf carbonate rock formations were exposed to karst weathering, leading to their very irregular topography of pinnacles and depressions, the latter becoming filled with sediment when sea levels subsequently rose. In the past 6000 years, when sea levels have been at about their present levels, wave and tide induced currents have been the principal influences on patterns of sedimentation.

Present day biological communities depend on substratum features at many different scales to provide solid anchorage points, vertical relief and increased availability of food items (through interaction with the physical processes driving modern day sediment deposition) (Kolasa 1989; Snelgrove and Butman 1994; Syms 1995; Williams and Bax 2001). Physical processes, including bottom current boundary layers and sedimentation of organic and inorganic matter, depend on the structural properties of these biological communities in addition to the underlying physical substrata (Snelgrove and Butman 1994). Mobile fishing gear has measurable short-term (weeks to years) effects on the structural components of habitat (reviewed by Rogers *et al.* 1998; Auster and Langton 1999) — removing or damaging epifauna, smoothing sedimentary bedforms, homogenizing mobile sediments (Schwinghammer *et al.* 1996) and disturbing or removing biota — e.g. calcareous red algae, bryozoans and corals — that create structure or substratum. The limited available data suggest that dragging fish traps, longlines and gillnets across the seabed has similar short-term effects, although restricted to a much smaller area (Rogers *et al.* 1998; Auster and Langton 1999).

Although the short-term direct effects of fishing have been well demonstrated, studies have rarely covered sufficient area or been continued for sufficient time, to show that effects of fishing gear have lasted beyond the short term and had flow-on consequences for associated invertebrate and fish communities. An exception is the work of Sainsbury *et al.* (1997), who assessed the importance of macroinvertebrate cover to fish communities on Australia's degraded North-west Shelf fishery. Their approach determined the potential (discounted) economic returns to the fishery of experimental fishing regimes (spanning up to 20 years) that incorporated area closures and annual surveys designed to clarify the link between habitat recovery and the composition and abundance of economically important fish communities.

Although it is recognized that fishing is the most widespread form of direct disturbance in marine systems below depths that are affected by storms (Watling and Norse 1998) and there is sufficient information to reduce that disturbance now, we do not (excepting Sainsbury *et al.* 1997) have the information necessary to manage fishing effects on habitat taking into consideration the costs of benefits of such actions (Auster and Langton 1999).

Part of the difficulty in determining and managing fishing (or any anthropogenic) effects on habitat is that habitat itself is poorly defined. It is subject to varying interpretations that make it almost meaningless in a decision-making framework without further qualification (cf. Yaffee 1999). Take for example the definition of essential fish habitat under the primary United States fisheries legislation where it is defined as: 'those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity' (US Magnuson–Stevens Act, 16 USC 1801 *et seq.* 1996). This is a definition that encompasses two-thirds of the planet. It is not obvious that this definition would assist managers in making decisions on marine resource management. It continues a species-centric approach to conservation that is increasingly seen as less valuable in comparison with the conservation of spaces or landscapes (Simberloff 1998; Roff and Taylor 2000 and references therein). In contrast, what is required is a habitat classification that represents the spatial distribution of the biological communities, but is based on features that are relatively easily mapped and managed, especially in data-poor situations typical of many marine environments. In this instance, we define habitat as the geological, environmental and biological structure that supports biological communities self-organized from the available species mix.

Several authors (e.g. Greene *et al.* 1994, 1999; Roff and Taylor 2000) have proposed a hierarchical, geophysical approach to classifying marine habitats. This approach recognizes that the structure and function of (marine) ecosystems is a multiscale process, that requires a multiscale management approach if conservation is to be effective (e.g. Holling 1992; Langton *et al.* 1995; Garcia-Charton and Perez-Ruzafa 1999; Poiani *et al.* 2000). It is the approach that we follow here.

We present habitat maps at three scales that relate to specific management needs. The first is a provincial scale (*sensu* Greene *et al.* 1999[1]) that provides the geological, sedimentary and hydrological properties of the continental shelf from 25 m to the shelf break (140–200 m). Mapping at

---

[1] Throughout this paper we describe the habitats by using the classification scheme developed by Greene *et al.* (1994, 1999). In this scheme *microhabitats* (e.g. solitary corals, small crevices, cms in size) lie within *macrohabitats* (e.g. kelp beds, boulders, 1–10 m) that lie within *mesohabitats* (e.g. reefs, bedrock outcrops, 10 m to km) that in turn lie within *megahabitats* (e.g. expanses of sediment-covered seafloor, submarine canyons, km to 10s of km or larger) that form part of a physiographic *province* (e.g. continental shelf, slope).

this scale provides the physical properties that correlate with the provincial scale regionalization of Australia's marine biological resources (IMCRA 1998), and the context in which to interpret the second level of mapping. At the second, megascale, level we map significant but irregular features of this province, using local fishers' information and opportunistic results from the provincial scale mapping survey. We interpret megascale features based on the observable geology and suggest which features, particularly important fishing grounds, are most likely to be vulnerable to physical disturbance. Lastly, we describe the mesoscale variability of particular (especially high-relief) megascale features. This is the level required to monitor effects and any remediation. In separate papers, we discuss the relevance of these scales and features to the communities of fishes (Williams and Bax 2001) and invertebrates (Bax and Williams 2000). By mapping at these three levels, we aim to provide a framework within which biological diversity, habitat, and the management of effects on it, can be more meaningfully discussed.

Methods

Sampling programme

There were three distinct components in our data collection (Bax and Williams 2000). First, we conducted a provincial scale survey of soft-sediment substrata where distances between study sites were large (10s–100s km) and sites were representative of large areas of the continental shelf (Fig. 1). Each site was coded by transect and depth [transects A–G, depth strata 1–5: 1(25 m); 2(40 m); 3(80 m); 4(120 m); 5(200 m)] and samples identified by a station code or codes. Second, we used these data, fishers' information and published data on unconsolidated seabed sediments and substrate geology of the area to develop basic seabed maps. Last, we focussed on six specific megahabitats, known to contain heterogeneous (soft-sediment and rock/reef) seabed types (Fig. 1). Detailed maps of bottom topography and acoustic reflectivity were used to differentiate substratum types, termed mesohabitats within megahabitats (Kloser *et al.* 2001). Cameras and physical and biological samplers were then used to measure the physical and biological characteristics of mesohabitats.

We recorded fishers' information for the megascale seabed map during a series of port visits (primarily to Lakes Entrance and Eden) and trips to sea on commercial vessels. General information on seabed types and extents of fishing grounds was combined with bathymetry and observations from early survey data and mapped in a GIS (MapInfo). This composite map was then returned to local fishers for review, before reaching its final form.

The locations of mesohabitat sampling sites were based on bottom topography and 'bottom-typing' acoustic indices from sounding surveys (see Kloser *et al.* 2001). In brief, Simrad EK-500 sounder echograms were examined visually at sea to delineate mesohabitats that contrasted with respect to two measures of the echo return (Orlowski 1984; Chivers *et al.* 1990). The first measure, index E1, is an integration of the tail of the first bottom echo, where the energy in the tail is assumed to consist of scattered reflections that increase from rugose substrata. The second index, E2, is an integration of the entire second bottom echo and provides a measure of the total energy reflected from the seabed and therefore a measure of acoustic reflectivity that increases from consolidated (hard) substrata. On this basis, contrasting mesohabitats in each megahabitat were nominally classified as relatively 'soft', 'hard' or 'rough'. Subsequent analysis of stored digital data from the 120 kHz transducer, corrected for sound absorbtion and one-way spherical spreading losses, quantified our *in situ* classifications (Kloser *et al* 2001). The E1 and E2 indices were mapped by using Vertical Mapper in Mapinfo (rectangular interpolation, cell size 0.005°, search radius 0.01°) for presentation.

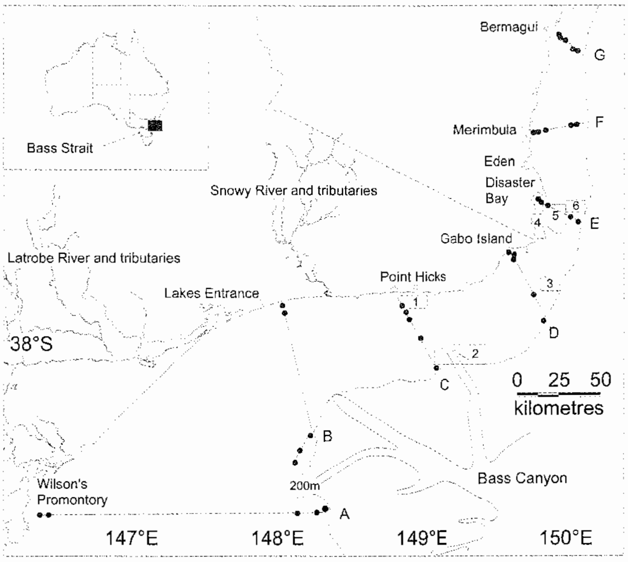


Fig. 1. Map of study area on the south-eastern Australian continental shelf, showing transects (lines, named at landward end), positions of depth-stratified stations (dots) and megahabitats (boxes) for the surveys. Megahabitats are: (1) Point Hicks; (2) The Horseshoe; (3) Gabo Reef; (4) Black Head; (5) Disaster Bay; and (6) Big Gutter. The rim of the Bass Canyon determined from recent swath mapping is shown in lieu of depth contours below 200 m, because published depth contours do not show this feature.

A novel towed camera platform, designed specifically for this study (Barker *et al.* 1999), was towed at constant height over all substratum types to collect remote and *in situ* video and higher resolution still images. Thirty-six hours of video and 5200 still photographs were collected along 79 km of seafloor transects. Video footage was generally high quality and 97% was suitable for analysis. Successful footage was obtained in rough sea conditions (up to 65 km h^{-1} wind-speed), and in strong ocean currents (2.8 km h^{-1}). The size of objects was estimated by comparison with paired laser beams of known separation. A description of the geomorphology and epifauna at each sampling site was made from the photographic images. Recorded attributes were based on the scheme of Greene *et al.* (1999) in conjunction with a set of semi-quantitative qualifiers when appropriate (Table 1). These semi-quantitative qualifiers are used consistently in describing different habitats in this paper.

Physical sampling

Soft sediments were collected by several different techniques — a Smith McIntyre grab, a pipe dredge and a modified 'Triple-D' demersal sled — because of sampling gear loss and gear development (Bax and Williams 2000). The grainsize was multi-modal for many samples, indicating that the samples were composed of sediments from different origins or had been deposited under two or more distinct current regimes. However, there was also some variation between replicate samples taken from a single station at different times. Whereas in some cases this represented small-scale variability in sediment size, in other cases, one or more samples had a truncated sediment frequency distribution. Fine sediments from these samples

Table 1. Data sheet used for recording habitat attributes from seabed images
Geomorphological features based on Greene *et al.* 1999

Gross morphology	Morphological modifiers	Bottom slope
Sediment	flat	slight (0-5)
Bars	regular ripples	sloping (5-30)
Banks	wavelength	steep slope (30-45)
Channels	amplitude	vertical (45-90)
Crevices	irregular	overhang (>90)
Debris field	(continuous, non-uniform)	
Ledges	hummocky	
Walls	(mounds/depressions)	*Elevation changes (m)*
Pinnacles	structure	
Slabs	(fractured/faulted)	pinnacles
Reefs	friable	walls
biogenic	outcrop	crevices
nonbiogenic	bedding	
	massive	
Bottom texture	**Textural modifiers**	**Bottom deposits**
organic debris	sorting	consolidation
mud (clay-silt)	packing	not-
sand (<2mm)	density	semi-
gravel (>2mm)	occasional	well-
pebble (>10mm)	scattered	erodability
cobble (>64mm)	contiguous	uniform
boulder (>256mm)	pavement	differential
bedrock	lithification	sediment cover
igneous	jointing	dusting (<1 cm)
metamorphic	rock roundness	thin (1–5 cm)
sedimentary	rock shape	thick (>5 cm)
	Process features	
Physical	**Biological**	**Communities**
currents	bioturbation	encrusting only
winnowing	tracks	mollusc beds
scouring	trails	ascidians
sediment trail	burrows	sea whips/sea pens
wave activity	excavation	sponge communities
upwelling	encrusters	crinoids
seismic	continuous (>70%)	*Maoricolpus roseus*
chemical	patchy (20–70%)	
cementation	little to none (<20%)	
weathering	communities	
oxidation		
General 'quantities'	*Misc. features/notes*	*General 'quantities'*
predominantly (>75%, many)	trawl tracks	sparse (<25% cover)
mostly (50–75%, several)		intermediate (25–50% cover)
some (50–25%)		dense (>75% cover)
occasional (<25%, few)		clumps
intermittent		individuals

may have been flushed during retrieval of the sampling gear; the samples were winnowed. As a result, we were concerned that we had failed to obtain representative samples with the Smith MacIntyre grab (our primary sampling device). The samples were, however, blast frozen upon collection and used to measure biological activity (reported here and in Bax *et al.* 2001). Previously published data were used for grain size distribution.

Ninety-nine sediment samples from Davies (1979), collected with a grab on an 18-km grid in the northern section of our study area, and from Jones and Davies (1983), sampled with a pipe or chain-bag type dredge at similar sampling intensity in the southern section, were reanalysed and mapped to show regional attributes. Samples were reported as being first wet-sieved into three fractions: greater than 2 mm (gravel); 2.0–0.062 mm (sand); and less than 0.062 mm (mud). To increase grainsize resolution, gravel was sieved, sand was analysed by using a settling tube, and mud was analysed by standard pipette analysis. The sample mean was determined by the method of moments, and inclusive graphic standard deviation was used as a measure of sorting (Folk 1974). The samples will have mixed sediments from the top 5–10 cm of bottom sediment.

Rock samples collected opportunistically during our provincial scale sampling were used to relate regional geology to acoustic data and the literature (e.g. Bernecker *et al.* 1997). Rock samples were also used to provide a geological description of some reef substrata that had been only sampled by video. Ten rock samples were slabbed and thin-section preparations made from off-cuts. Description and classification were based on colour, induration, dominant skeletal components, sorting and sedimentary structures.

Frozen sediment samples were prepared for carbonate analysis by washing in distilled water, drying overnight, and weighing before adding 1 M HCl and again leaving overnight. The acid was removed and the sediment washed until neutral pH attained. The dried sediment was re-weighed, the difference in weights givng the amount of carbonate in the sample. Organic content was determined by combusting at 480°C. The amount of material burnt off was considered equivalent to the organic component of the sediment.

Stable isotope ratios in the sediments were measured to identify the source of biological material. Frozen samples were thawed, washed in distilled water (to remove salt) and dried. Samples for stable carbon analysis were soaked in 1 M HCl overnight (to remove carbonate), rinsed several times until a neutral pH was attained, then dried. Dried sediments were analysed separately for stable carbon and stable nitrogen by using standard methods. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per-thousand (‰) difference between the sample and conventional standards (the primary standards are Pee Dee Belemnite, a marine limestone fossil, and N_2 in air):

$$\partial X = \left[{}^{R_{\text{sample}}}\!\big/\!{}_{R_{\text{standard}}} - 1 \right] \times 1000$$

where X is ^{13}C or ^{15}N, and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Invertebrate cover was estimated visually from the video footage on a semi-quantitative scale, whereas the identity of the invertebrates was determined from samples taken with a demersal sled (Bax and Williams 2000). Many of the invertebrate taxa in the area are undescribed. To ensure consistent identifications, we developed a classification based on taxonomy and morphology with only 71 categories (Bax and Williams 2000). Animals were identified to the lowest possible taxa (which under field conditions varied between phyla and species) then aggregated on the basis of their morphology (e.g. soft, fenestrate and hard for bryozoans).

Results

Level 1. Provincial scale sampling of susbstrata

Distribution and composition of soft sediment substrata

The soft sediments consist primarily of sands, with gravels making up a higher proportion in the south. Generally, inner-shelf sediments (≤40 m) are less stable, more sorted and rippled by water currents and storm events. Outer shelf sediments (≥80 m) are more stable, have higher levels of bioturbation and are less rippled by water currents; mud is present in localized areas (Plate I and Table 2).

Organic matter in the sediment increased with depth ($r = 0.51$, $P < 0.0001$, $n = 117$). Inshore sites had as little as 0.2% organic matter in the sediment. The highest level of organic matter (5.3%) was found at the 40 m site (B2) on the Lakes Entrance transect but in general, the highest levels of organic matter on each transect were found at the 120 or 200 m site (depth strata 4 or 5). There were significant and strong relationships between grain size and the amount of organic matter in the sediment ($r = 0.71$, $P < 0.0001$, $n = 41$); finer sediments contained more organic matter.

Stable carbon ($\delta^{13}C$) in the sediment averaged –21.9 ± 0.9‰ (s.e.), which is in the range expected from material obtained from temperate marine phytoplankton (–24 to –18‰; Fry and Sherr 1984). Organic matter and stable carbon were strongly related ($r = 0.56$, $P < 0.0001$, $n = 92$), values for both characteristics increasing with increasing depth.

The most consistent depth-related trend for all measured sediment characteristics was the strong correlation ($r = 0.72$, $P < 0.0001$, $n = 96$) between depth and the amount of carbonate in the sediment. Inshore sites had as little as 1.2% carbonate and shelf break samples contained up to 97.1% carbonate. There was a strong relationship between carbonate and organic matter ($r = 0.62$, $P < 0.0001$, $n = 95$): sites with high levels of carbonate had higher levels of organic matter. The relationship between carbonate and $\delta^{13}C$ in the sediments was strong ($r = 0.55$, $P < 0.0001$, $n = 94$).

Sand and gravel are characteristic of the entire study region south of Cape Howe (Jones and Davies 1983). Reverse-sorting (coarser grains seaward) is the regional pattern up to Jervis Bay, 150 km north of the study area (Jones and Davies 1983), with fine sand dominant along the inner-shelf, medium-grained sand further seaward and locally coarse sand or, less frequently gravel, at the shelf break. Terrestrial sediment input to the region is low; Australia is a dry continent with low relief. Discharge from the several small rivers entering the area is small. Annual flow of the largest river in the area, the Snowy River, was reduced to 0.5–4.0 km^3 between the 1950s and 1970s when it was diverted to produce hydroelectric power.

The reverse-sorting pattern is disrupted in the study area by several extensive areas of very fine sand and mud. One is offshore from Lakes Entrance and the others are close to the shelf break, especially in areas such as the 'Horseshoe' situated at the head of an arm of the Bass Canyon (Fig. 1). Many of the sediments in the area are poorly sorted (standard deviation more than 1.0 φ) because of their mixed terrestrial, marine and biological origins.

Five sediment types have been described (Jones and Davies 1983), although their boundaries are often not distinct. The five principal sediment types in the area (Fig. 2) are: inner-shelf quartoze sands; outer-shelf fine grained shelly sands; bryozoan sands and gravels; muddy sediments; and shelf-break gravels.

The well to medium sorted quartoze sands of the inner-shelf are modern and more-or-less in equilibrium with present conditions; newly deposited sediments are qualitatively similar to resuspended sediments. They are dominantly unimodal suggesting a single transporting mechanism, and the carbonate component consists of freshly broken shell debris.

Offshore of the inner-shelf quart-zose sands, are poorly sorted, slightly quart-zose, fine shelly sands in which relict and modern components are present in about equal proportions. They vary greatly in textural characteristics but always contain some quartz and are nearly always polymodal with a mixed faunal assemblage that includes both modern and relict components. These sands are poorly sorted and the evidence is that they are transitional in nature, adjusting from lower sea level stand conditions to modern conditions. The better sorted of these sands are approaching equilibrium with the present-day environment.

Bryozoan sands and gravel cover extensive areas of the outer-shelf in the southern part of the study area and are mainly relict, although a significant amount is contributed by the modern benthos. The sands are usually poorly or very poorly sorted and polymodal. Their main constituents are texturally and compositionally unrelated to the present environments.

The extremely poorly sorted muddy sediments of central Bass Strait and the south-eastern Victorian and Tasmanian shelves occur in water depths ranging from 44 to 212 m (Jones and Davies 1983). Mud zones on the eastern Australian shelf occur off river mouths (Davies 1979) and, because they are deposited over areas exposed during the most recent Ice Age low sea level stand (areas of the shelf shallower than present day depths of 140–150 m), date from the late Holocene (0–10 000 years ago). The presence of muddy sediments at greater depths (down to at least 220 m) at the heads of the Bass Strait canyon suggest that uplifting of slope sediments is a second source of shelf muds. Upwelling is a feature of the southern part of the study area (Edwards 1990; Bax *et al.* 2001).

The shelf north of Cape Howe (and south of Jervis Bay) is narrow and shallow, with the shelf-break at about 140–150 m. The continental slope is steep, and both slope and outer-shelf show evidence of major erosion. The coarse shelf edge gravels, the high shelf-break, the abundant evidence of erosion, and the fine-to-coarse textural gradient point to the sediments being relict from at least the last sea level low, >10 000 years ago (Davies 1979).

Distribution and composition of consolidated rock/reef substrata

Fossiliferous limestones and sandstone comprise the majority of rock/reef substrata in the study area (Fig. 3). The main limestone regions include: the extensive Howe and Gabo Reef and Broken Reef complexes; the major elongate outcrops adjacent to the present day Gippsland coastline (see under sandstone); many unnamed reef patches off the southern NSW coastline; numerous scattered small outcrops throughout the study area; and patchy hardgrounds including the Flower Patch.

Limestones are most conspicuous as relatively large megahabitats (km to 10s of km in length), with a flat, raised (<2 m), tabular slab form. However, cemented carbonates also form low-lying hard grounds that are bored and encrusted by benthic organisms. These are likely to form 'patches' or mosaics of hard substratum that show little (<20 cm) or no vertical relief. Two examples are the low-relief limestone South-east Reef (Plate II*d*), and 'bryozoan reefs', constructed primarily from bryozoan clasts, that form relatively small patches on mobile substrata towards the shelf-break. The latter support stands of stalked crinoids (Plate II*i*) and characterize areas including the Flower Patch, named as such because of the stalked crinoid 'flowers' that came up in fishers' nets (Fig. 3). Limestone reefs in shallower reaches of the shelf have been exposed to the air during sea-level regressions and show signs of karst weathering (Fleming and Roberts 1973; Bernecker *et al.* 1997). Weathered reefs have a more irregular topography with large pinnacles and depressions and are evident in sections of the Broken Reef complex (Fig. 3 and Plate II*c*).

Quartz-rich, coarse-grained sandstone crops out as tabular slabs adjacent to areas of soft sediments off the Gippsland coastline (Fig. 3). Sandstone (together with fossiliferous limestone) occurs as elongate, low-relief slabs which are parallel to the present-day Gippsland coastline (Fig. 3), and sandstone is likely to be a common constituent of 'reefs' (banks in geological terminology) further offshore, e.g. the outer-shelf Broken Reef complex (Fig. 3).

Tertiary (2–65 million years old) soft sediments flank older, previously eroded Devonian granite (345–395 million years old) outcrops on the inner-shelf off the Gippsland coastline. These eroded outcrops have high-relief (>10 m) and are distinctive in being formed of irregular, hexagonally jointed, coarsely crystalline granite. They form the relatively localized, hard 'reefs' at Point Hicks (Plate II*b*) and the New Zealand Star Banks (and are probably lateral submarine extensions of the adjacent granitic Point Hicks (Fig. 3).

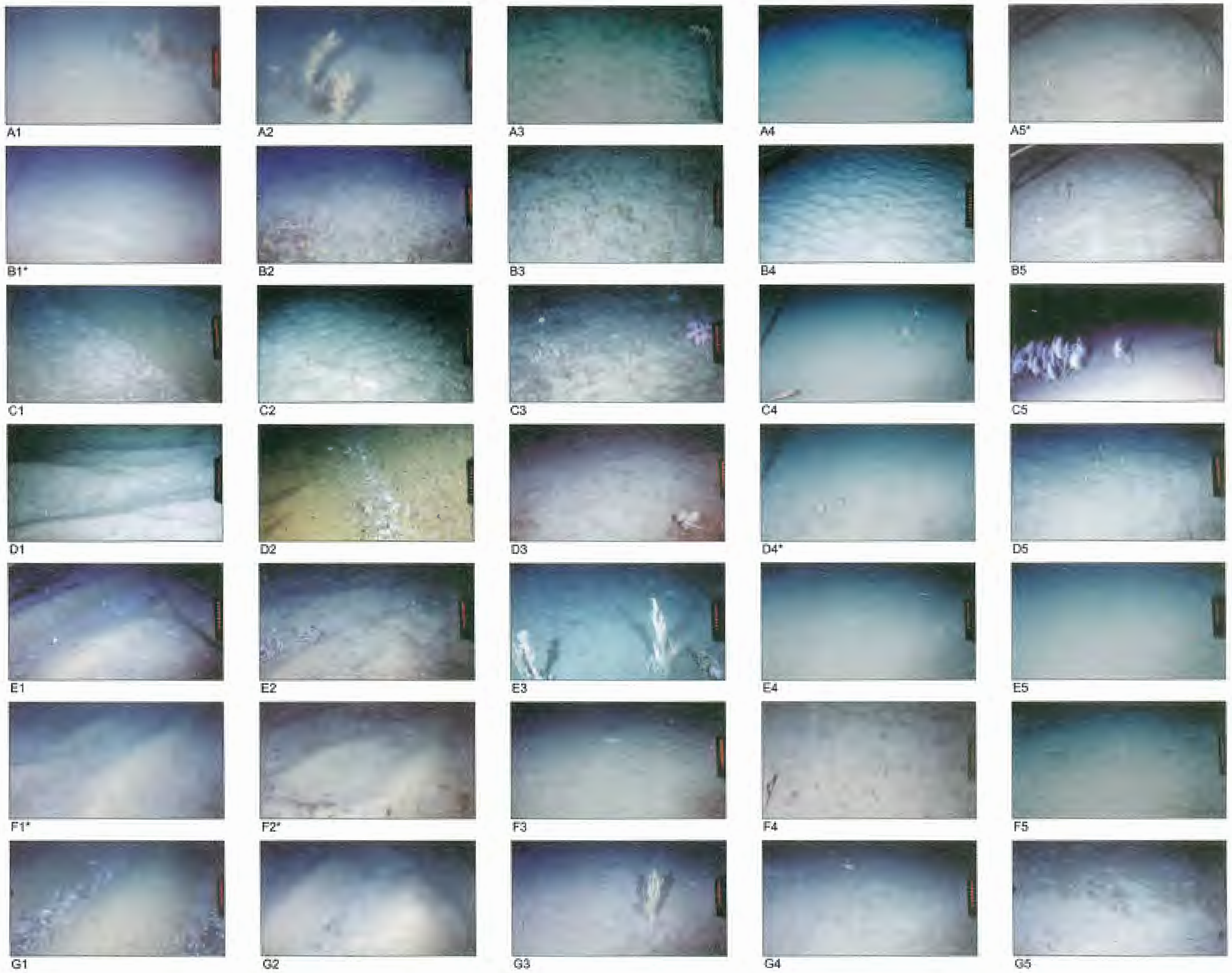


Plate I. Representative picture of substratum at each provincial scale sampling station. First letter in picture identifier is transect (see Fig. 1); second is cross-shelf position (depth): 1(25 m); 2(40 m); 3(80 m); 4(120 m); 5(~200 m). *, indicative, based on video footage but taken at an adjacent station.

Table 2. Distinguishing physical and biological characteristics of provincial-scale sampling station

Transect			Depth		
	1 (25 m)	2 (40 m)	3 (80 m)	4 (120 m)	5 (200 m)
A	Thick unconsolidated muddy sand. No slope. Intermittent bushy sponge indicates underlying harder substrate	Thick unconsolidated muddy sand. Slight slope. Irregular depressions (~30cm deep). Intermediate bushy sponge. Wave scouring. Bioturbation	Thick, semi-consolidated mud. Slight slope. Intermediate worm tubes and sparse ascidians. Overlay of organic debris. Bioturbation	Thick semi-consolidated mud. Slight slope. Intermediate worm tubes and sparse ascidians. Bioturbation with occasional burrowing and excavation	No video footage
B	No video footage	Poorly-sorted, unconsolidated, thin mud over shell fragments. Slight slope. Sparse to dense mollusc beds incl. *Pecten* spp., *Chlamys* spp., and *M. roseus*	Thick semi- to well-consolidated mud. Slight slope. Sparse ascidians, dense worm tubes, occasional soft coral. Bioturbation with some burrows and excavations	Unconsolidated mud over shell fragments. Slight slope. Intermediate worm tubes and intermittent ascidians. Irregular small-scale (<10cm) mounding	Semi-consolidated thick mud and organic debris. Slight slope. Sparse ascidians (*Polycarpa* spp.) and sea pens. Some bioturbation with small depressions
C	Unconsolidated poorly-sorted sand with shell fragments. Slight slope. Large (50cm) wavelength and small (10cm) amplitude ripples. Dead *Pecten* spp. and glycimerid bivalves. Some bioturbation	Unconsolidated sand bottom. No slope. Medium ripples. Shell fragments in troughs. Sparse *M. roseus*. Occasional bioturbation	Semi-consolidated thick mud with organic debris. Slight slope. Intermediate worm tubes. Occasional seastar, ball sponge, stalked ascidians (*Pyura* sp.), soft bryozoans and hermit crabs	Well-consolidated, thick mud. Slight slope. No ripples. Sparse worm tubes. Some bioturbation with small burrows	Thick mud with organic debris. Slight slope. Intermittent stalked crinoids on hard substrate. Occasional pancake urchins and small ascidians. Intermittent bioturbation
D	Unconsolidated sand and shell fragments. Intermittent biogenic reef. Medium ripples. Dense sponge and brown alga on reef. Algae on undisturbed sand. Occasional bioturbation	Unconsolidated coarse-medium well-sorted sand. Shell (*Pecten* spp., mussels, bivalves) in troughs. Large ripples. Sparse worm tubes and occasional *M. roseus*. Occasional bioturbation	Semi- to well-consolidated mud with organic debris. Slight slope. Intermediate worm tubes, individual ascidians and occasional lumpy sponges on dead shell	Thick mud with organic debris. Slight slope. Some small (10cm) mounds and depressions. Occasional individual ascidians. Bioturbation	Thick, well-sorted mud. Slight slope. Sparse yellow ascidians (*Polycarpa* spp.) and sea pens
E	Sand and shell fragments. Regular medium ripples. Empty shells (mostly glycimerid) in troughs. Occasional bioturbation with minor reworking in sand mounds	Semi-consolidated moderately sorted muddy sand. Regular medium ripples with worm tubes on crest; bryozoan and shell fragments in troughs. Intermittent low branching sponge. *M. roseus* patches	Well-consolidated thick mud with organic debris. Slight slope. Occasional irregular bushy and branching sponge. Intermittent seastars, urchins and whelks. Intermediate to dense worm tubes. Some bioturbation	Well-consolidated thick mud with organic debris. Slight slope. Occasional seastars and irregular bushy and branching sponges. Intermediate worm tubes. Occasional bioturbation	Well-consolidated thick mud with organic debris. Slight slope. Sparse ascidians and sea pens. Some bioturbation
F	No video footage	Well-consolidated thick mud with organic debris. Slight slope. Patchy medium ripples. Occassional but dense *M. roseus* beds and worm tubes. Occasional sponge. Irregular mounds and depressions	Well-consolidated thick mud with organic debris. Slight slope. Intermediate worm tubes. Intermittent sponge and seastar. Some bioturbation	Semi-consolidated thick mud/shell with organic debris. Slight slope. Intermittent small sponges. Some bioturbation and occasional excavations	Semi-consolidated thick mud with organic debris and unconsolidated poorly sorted shell and bryozoan fragments. Slight slope. Sparse ascidians (*Polycarpa* spp.), seawhips and worm tubes
G	Sand/gravel. Intermittent mud patches. Med. ampl. large wavelength ripples and banks. Shell fragments in trough. Irregular mounds and depressions in mud patches. Intermediate *M. roseus* on sand/gravel; occasional on mud	Semi-consolidated muddy sand. Slight slope. Regular med. ampl. Large wavelength ripples. Fine shell fragments in trough. Occasional bioturbation and excavation	Semi-consolidated thick mud with organic debris. Slight slope. Occasional sea stars, urchins, ascidians, irregular and bushy sponge. Occasional bioturbation and excavation	Semi-consolidated thick mud with organic debris. Slight slope. Occasional bioturbation and excavation	Well-consolidated thick mud with organic debris. Slight slope. Some areas of bryozoan clasts and mollusc shell with attached small sponge and ascidians (*Polycarpa* spp.) Intermittent bioturbation and excavation

Notes: Sediment thickness: <5cm, thin; >5cm, thick.
Ripple size: <10cm, small; 10–30 cm, medium; >50 cm, large. Wavelength: amplitude unless otherwise stated.
M. roseus: Maoricolpus roseus.

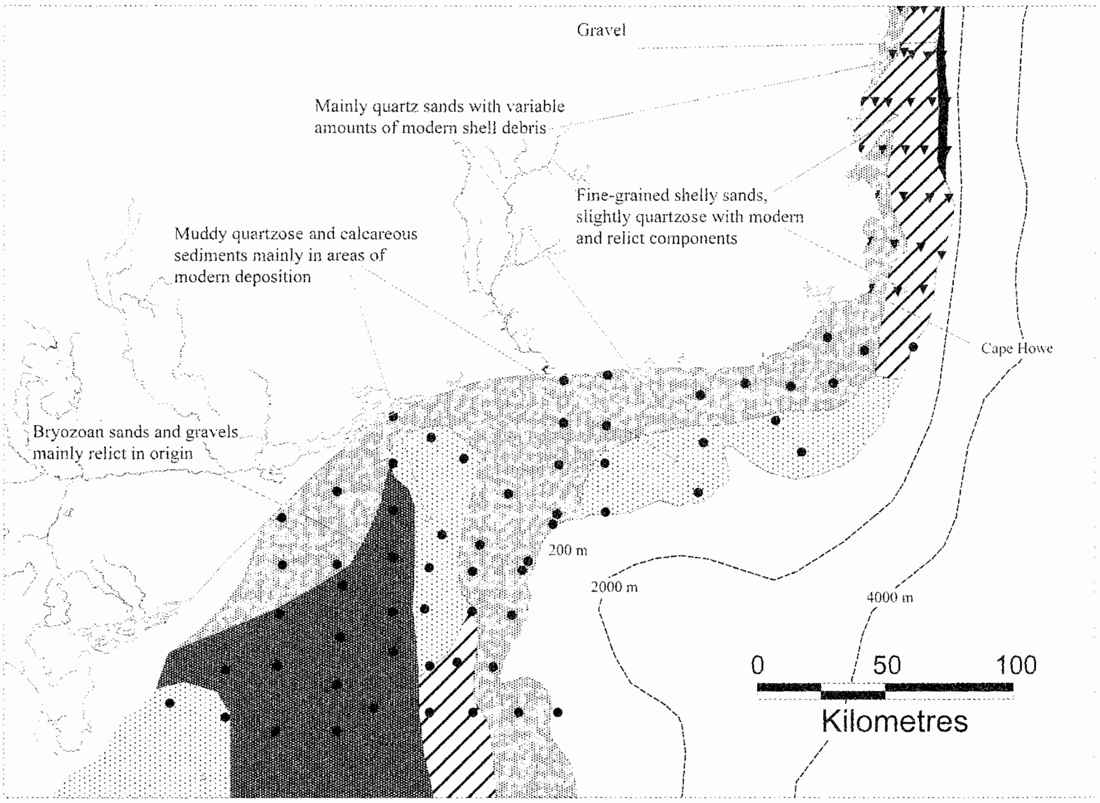


Fig. 2. Map of sediment types in the sampling area based on published data (Davies 1979, triangles; Jones and Davies 1983, circles). Depth contours below 200 m are indicative only.

Level 2. Megascale mapping of the seabed

The megascale map of the major seabed features constructed from the conjunction of information provided by the fishing industry (general substratum types and dominant invertebrates or fishes) and our early survey data (geomorphological descriptors and bathymetry) is shown in Fig. 4. This megascale map facilitated the selection of megahabitats, and the means to extrapolate the spatial extent of the megahabitats identified by our samples. Megahabitats are, to a large extent, synonymous with fishing grounds. Most of the names used are those of the local fishers.

Level 3. Delineating mega- and mesohabitats

Six megahabitats were mapped with acoustics (Kloser *et al.* 2001) (Fig. 1). Visual observation of acoustic echograms linked with GPS provided good initial discrimination of three relatively distinct mesohabitats – nominally soft, hard and rough – within each megahabitat.

Point Hicks megahabitat

This megahabitat bounds an inner-shelf (~40 m depth) region off the Gippsland coastline at Point Hicks (Fig. 1) and consists of a granite outcrop and an adjacent sediment flat. The Broken Reef complex lies seaward of the sediment flat, with the shelf-break including the Horseshoe beyond.

The soft mesohabitat is mostly sand with regular, small (<10 cm) wavelength and small (<10 cm) amplitude ripples and some areas of shell bed (Plate I C2). There is noticeable small spatial scale variability in ripple structure and some areas of large (>30 cm) wavelength and large (>30 cm) amplitude regular wave patterns were observed on one survey. The bottom was unconsolidated with shell fragments accumulated in the troughs of the ripples. There were occasional beds of *Maoricolpus roseus* with densities ranging from intermediate to sparse, and occasional signs of bioturbation with a variable, but generally sparse, density of excavations.

The rough mesohabitat is a rock outcrop close to the shore and inshore of the soft mesohabitat. It is predominantly granite, mostly boulders with rounded surfaces, creating crevices and steep slopes (Plate II*b*). At the margins of the boulders there is predominantly thick (>5 cm), well consolidated, well sorted sand and gravel with occasional low-relief (<1 m) limestone reefs. There were regular ripples of medium amplitude and wavelength (10–30 cm) and intermittent signs of scouring around reefs. A coarse, shell debris filled the ripple troughs. Dense epifaunal communities, including encrusting and erect sponges, occasional seawhips (*Primnoella australasiae*) and calcareous red algae, were present on the consolidated substrata. No intermediate 'hard'

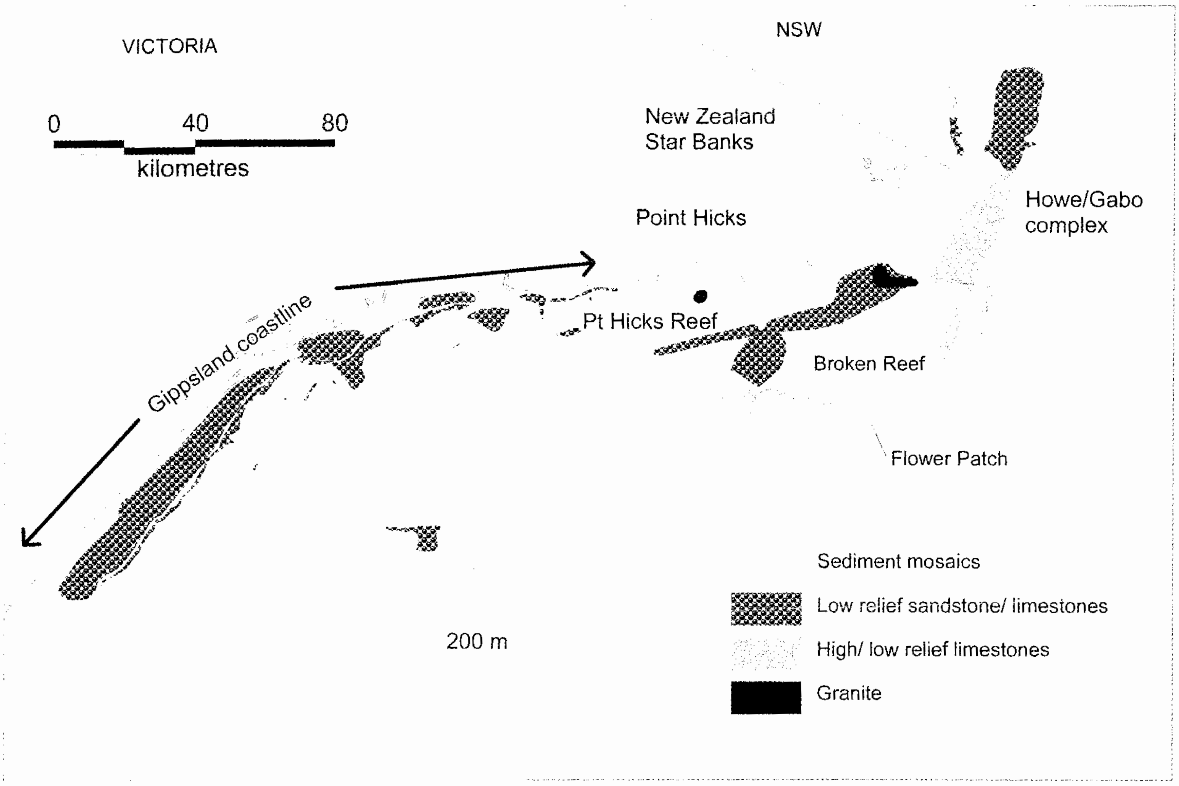


Fig. 3. Megascale map of primary substrata on the south-eastern Australian continental shelf.

mesohabitat was delineated because the sediments flank the rock/reef outcrops.

Black Head megahabitat

This megahabitat lies at 40–50 m depth off the headland of the same name (Fig. 1). It is bounded inshore by coastline reefs, and offshore by the extensive sediment flat of Disaster Bay.

The soft mesohabitat is an extensive area of semi-consolidated sand and mud with regular ripples of medium (~10–30 cm) amplitude and wavelength, on a gradually sloping bottom (cf. Plate I E2). Ripples suggest wave action or currents modified the sediment, but probably only during high wave or storm activity as there are signs, in the form of worm tubes forming along the crests of the ripples, that the sediment has been stabilized. Sediment sorting was moderate with bryozoan and shell fragments in ripple troughs. Low branching sponges occurred intermittently (<5% occurrence) and there were intermittent to occasional (<25 % occurrence) *Maoricolpus roseus* communities in intermediate densities (25–50% cover). Possible changes to sediment topography by *M. roseus* are suggested by consecutive reference photographs of an area with and without *M. roseus*.

The hard mesohabitat is an area of scattered limestone slabs and boulders with a dusting of well sorted mud and sand on a gradually sloping bottom with intersecting patches of apparently thick (>5 cm) unconsolidated sand. Sediments have regular non-symmetrical ripples of small wavelength (<10 cm) and small (<10 cm) amplitude. There was an intermediate to dense cover (25% to >75%) of sponges (predominantly finger sponges) on limestone outcrops, areas with thin sediment cover, and occasional boulder patches.

Slabs of fossiliferous limestone reef with crevices and ledges, occasionally interrupted by small areas of thin (~1–5 cm), moderately sorted, unconsolidated fine sand form the rough mesohabitat (Plate II*a*). The reef is mostly flat, but has some pinnacles and walls (~1–3 m) with some steep to vertical slopes. A few areas were strewn with boulders. The reef had a dusting (<1 cm) of organic debris and silt, and was mostly covered by occasional seawhips and dense communities of patchy encrusting sponges, intermittent cup sponges and broad irregular fronded sponges. Finger sponges occurred where bedrock was exposed in the small areas of sediment.

Disaster Bay megahabitat

This megahabitat is in the eastern part of Disaster Bay at approximately 80–100 m depth and adjacent to the western margin of the Howe and Gabo Reef complex (Figs 1 and 4). The Bay extends for a considerable distance inshore, shelving gradually to the coastline south of Cape Howe.

The soft mesohabitat is an extensive area of unrippled, thick (>5 cm) semi to well consolidated mud with some

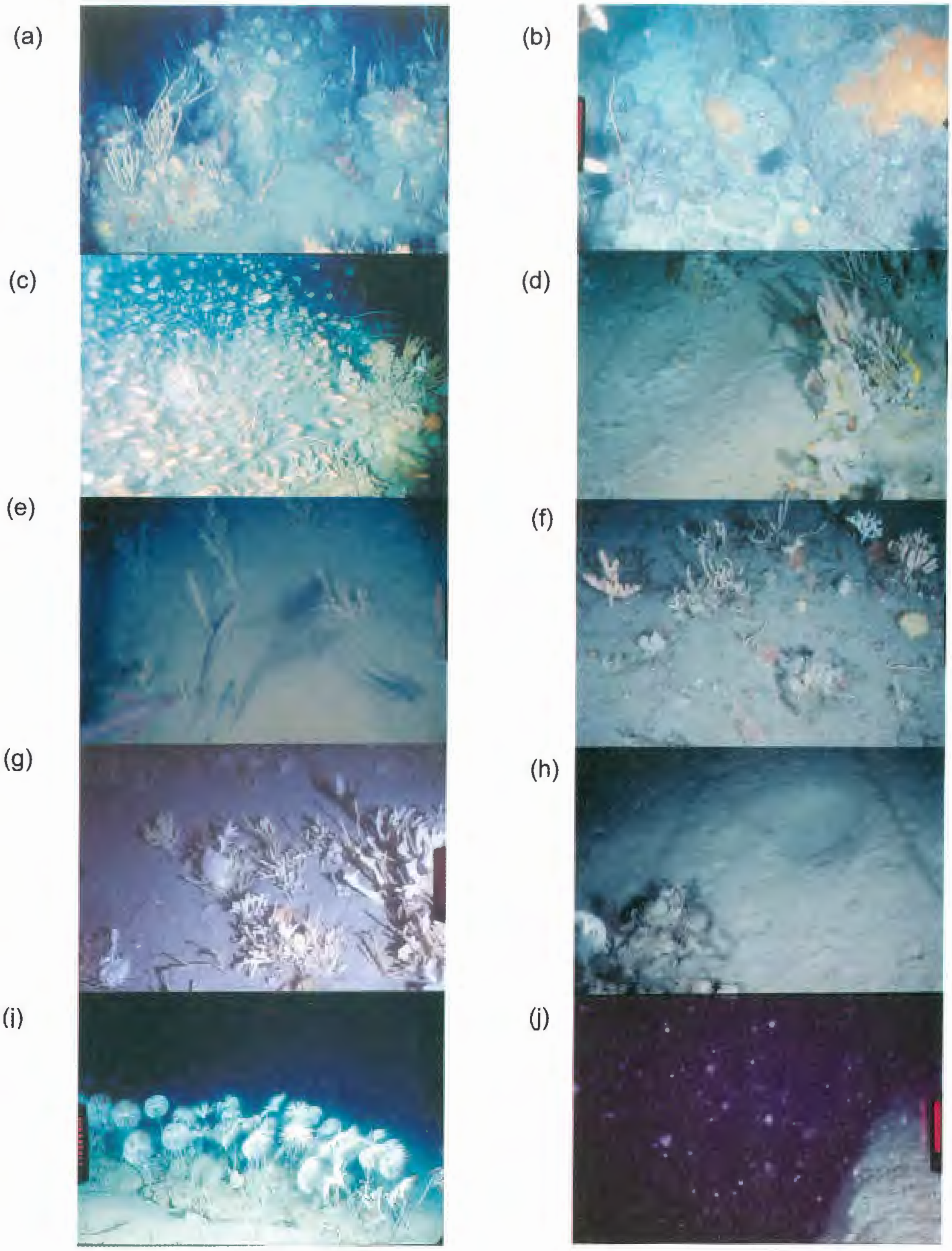


Plate II. Representative images of consolidated sediment and rock/reef seabed habitats on the south-eastern Australian continental shelf (see also high-relief limestone at Gabo Reef, Plate III): *(a)* low-relief limestone, 'rough' mesohabitat of Black Head Reef at ~40 m; *(b)* margin of granite outcrop, 'rough' mesohabitat of Point Hicks Reef at ~40 m; *(c)* low-relief limestone, shoreward section of Broken Reef at ~70 m (with schools of juvenile redfish (*Centroberyx affinis*); *(d)* low-relief limestone, South East Reef at ~70 m; *(e)* semi-consolidated sediments around scattered limestone, 'hard' mesohabitat of Disaster Bay at ~80 m; *(f)* low-relief limestone, seaward section of Broken Reef at ~90 m; *(g)* platform of low-relief limestone, 'rough' mesohabitat of Howe Reef at ~100 m; *(h)* bioturbated sediment and bryozoan reef, 'hard' mesohabitat of The Horseshoe at ~140 m; *(i)* bryozoan reef and consolidated sediment supporting stalked crinoids (*Metacrinus cyaneus*), the Flower Patch at ~160 m; *(j)* exposed basement rock at precipitous continental shelf edge, Little Horseshoe at ~190 m.

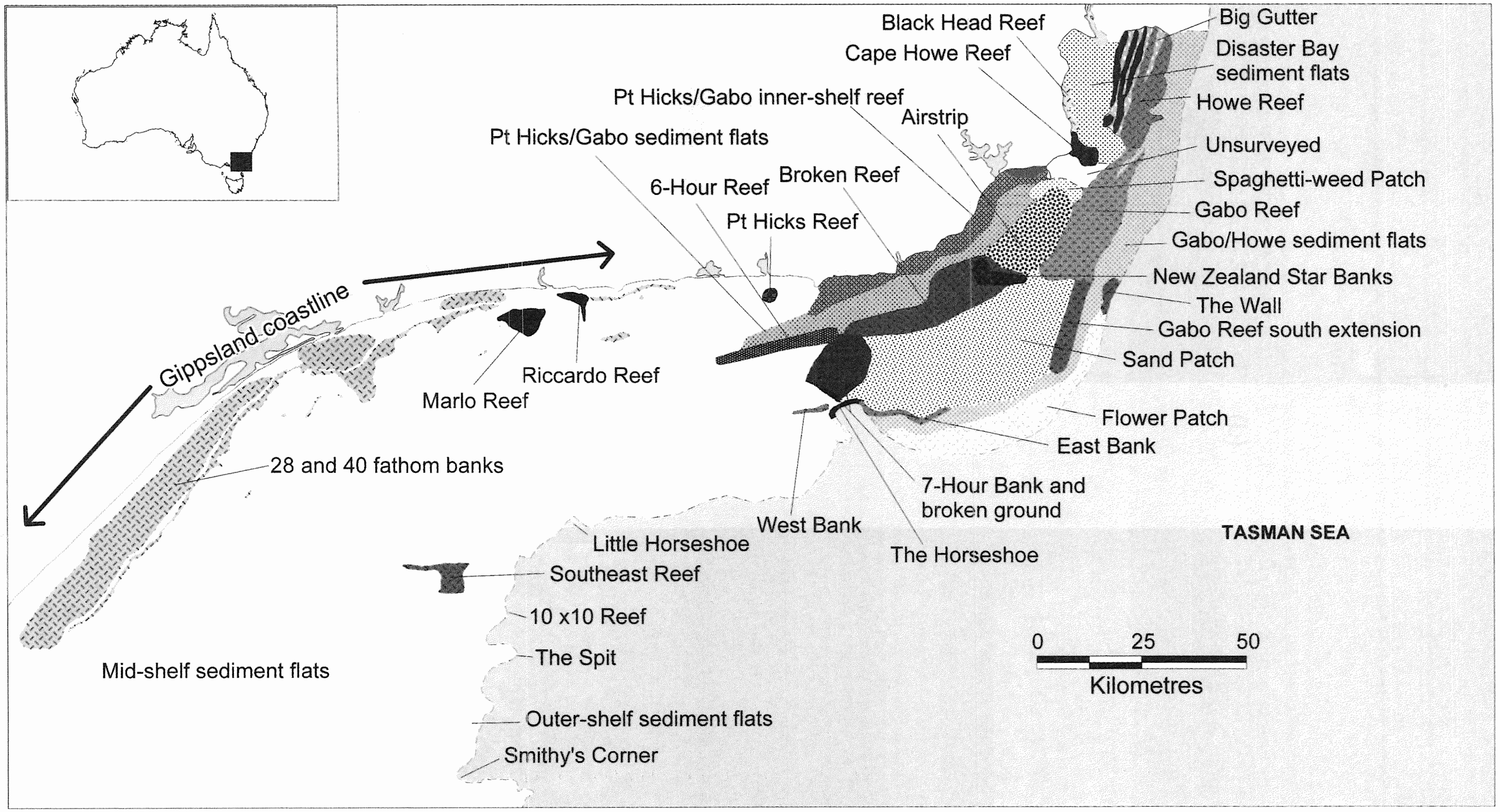


Fig. 4. Megascale map of seabed habitats on the south-eastern Australian continental shelf based on information supplied by the fishing industry and provincial-scale survey data.

organic debris (sponge fragments and worm tubes) on a gradually sloping bottom (Plate II E3). A sparse to intermediate cover of irregular, yellow bushy sponges and intermittent seastars, urchins and whelks was seen at the inner margins (off Black Head) but only isolated individuals elsewhere. Bioturbation was evident with occasional small depressions from burrowing infauna. There were occasional straight, parallel furrows in sediment caused by the bobbins, rollers and doors of trawls.

An area of gradually sloping, flat, mostly thin (<5 cm) mud with occasional slabs of fossiliferous limestone forms the hard mesohabitat (Plate II*e*). Clumps of large bushy sponges and some seawhips (*Primnoella australasiae*) were attached to the slab outcrops, and occasional small yellow ascidians (*Polycarpa* spp.) occurred on sediments.

The rough mesohabitat is a fossiliferous limestone slab reef. Reef margins were not seen clearly but are likely to be similar to the reef seen at the Big Gutter, a few kilometres to the east (Fig. 4). There are some high-relief (>3 m) reef patches with pinnacles, but more generally the reef is relatively low relief with a thin (<5 cm) cover of mud with sparse epibenthos. Where distinct, the margin is characterized by outcrops of hard substratum densely covered with sponges and seawhips. Adjacent muddy sediment was well consolidated and sorted and some bioturbation including small excavations was observed.

Big Gutter megahabitat

This megahabitat is a central section of the Howe Reef in ~80–100 m depth, where the reef is broadly subdivided by channels running approximately SSW–NNE, the commercial 'gutter tows' of which Big Gutter is one (Figs 1 and 4). Disaster Bay is to the west (inshore), and offshore of the reef a sediment flat extends to the shelf-break.

The soft mesohabitat is an area of unrippled, well sorted, semi-consolidated, thick (>5 cm) mud and organic debris offshore of the reef in ~125 m depth (Plate I E4). There were intermediate levels of bioturbation with some burrows and trails and occasional individual solitary ascidians. The absence of sediment patterns indicated minimal wave or current activity, although some trawl tracks were observed. The 'hard' mesohabitat is the floor of Big Gutter, a commercial trawl tow. It is an extensive area of predominantly unrippled, well sorted, unconsolidated mud with some organic debris. Some low-relief (<1 m) slabs of biogenic (fossiliferous limestone) reef protrude from the gradually sloping bottom. There was some bioturbation, worm tubes and a sparse (<25%) cover of ascidians, seawhips (*Primnoella australasiae*) and sponge communities (including sea fans and bryozoan).

A fossiliferous limestone slab reef forms the rough mesohabitat (cf. Plate II*g*). The reef edge has a variable morphology with vertical slope and overhangs. Its margin is distinct in places, with some patches of high-relief substratum (>3 m) with pinnacles, some of which support a dense cover of sponges and seawhips. Other areas have a less distinct margin and a steep slope (30–45°). The reef platform has a thin (<5 cm) mud cover with sparse epibenthos and some evidence of bioturbation including small excavations.

Gabo Reef megahabitat

This megahabitat is on the outer edge of a southern section of an extensive fossiliferous limestone reef at ~100–130 m depth (Figs 1 and 4, and Plate III*a*). This reef is a complex that continues inshore (westward) to connect with the 'Airstrip' sediment flats and northwards to connect with the Howe Reef. To the east the soft mesohabitat extends out to the shelf-break.

The soft mesohabitat (Plate III*b*) is an extensive area of gradually sloping, unrippled, well consolidated, thick (>5 cm) mud with organic debris. It is bioturbated and has a sparse cover of ascidians and sea pens.

The reef margin forms the hard mesohabitat (Plate III*c*). Some sections of the reef margin are steep (45–90°), high-relief walls (>3 m) with ledges, overhangs and crevices, whereas others slope gradually over a broken boulder substratum. Some sections of the reef edge are >10 m above the adjacent sediment flat. Occasional sponge communities were observed on reef outcrops. The abundance of sponges increased close to the reef edge where more hard substratum suitable for attachment is exposed. Epifauna included occasional large cup sponges, prostrate plate sponges and highly branched finger sponges. Immediately adjacent to the reef edge, a thick cover of unconsolidated mud on hard substratum forms the shoulder of the reef. Sponge cover was sparse to intermediate in this area with some bioturbation and sediment reworking.

The rough mesohabitat is the reef platform (Plate III*d*). The surface is irregular and slightly hummocky with small pinnacles (0.5–1.0 m) and occasional small, undercut outcrops (~1 sq m) and is mostly overlain with a thin (<5 cm) cover of unconsolidated mud. An intermediate to dense cover of sponge communities (finger and cup sponges) and occasional pancake urchins (*Phormosoma* sp.) was observed where sediments were thin or the reef exposed.

The Horseshoe megahabitat

The Horseshoe is the shelf-break rim of a major head of the Bass Canyon (Fig. 1). Three sites around the canyon rim in ~150–180 m depth were sampled: a well defined, but small (<2 km in length) elevated rock structure on the western margin south of the West Bank (rough mesohabitat); an area within the 'Flower Patch' characterized by stalked crinoids on the eastern margin (hard habitat); and an adjacent area of sediment flat on the western margin (soft habitat) (Fig. 4).

The soft habitat is an extensive area of thick (>5 cm) unrippled mud and organic debris on a flat bottom (<5°

slope). There were intermittent signs of bioturbation including excavations on the soft habitat, occasional pancake urchins (*Phormosoma* sp.) and small ascidians.

The hard mesohabitat is predominantly a gradually sloping unconsolidated mud sediment with occasional outcrops of low-relief, cemented sediments, limestone slabs and bryozoan reef (Plate II*h*). There was a dusting (<1 cm) of mud on outcrops, and evidence of scouring around their bases. Bioturbation was evident in the unconsolidated mud sediment with tracks, trails and burrows, together with a sparse cover of seapens and pancake urchins. There was an intermediate cover of stalked crinoids on most pieces of hard substratum (Plate II*i*) together with occasional sponges, ascidians and gorganacean soft corals.

The rough mesohabitat is an area of lithified limestone flanked by predominantly unrippled, well sorted, unconsolidated, gradually sloping mud. The slabs have intermittent overhangs (<0.5 m), and there were local areas of sediment scouring. There was a sparse cover of sponges, seawhips (*Primnoella australasiae*) and stalked crinoids on the hard substratum and some ascidians were observed. Bioturbation was intermittent with excavations and hollows visible.

Discussion

At a resolution of 10s of kilometres, the seascape of the south-eastern Australian continental shelf can be visualized as a series of massive sediment flats ('soft-grounds') with reefs, bedrock and consolidated sediments ('hard-grounds') cropping out in dispersed patches. In our study area, sediment flats comprise the vast majority of the seabed (89%), with prominent hard-grounds making up only 11% (Bax and Williams 2000). Additional outcrops of reefs and banks (biogenic and bedrock) and patches of cemented hardgrounds in the sediment flats, would be identified at a finer-scale resolution (100s of metres), particularly at the shelf-break. However, they would not substantially alter the overall proportional areas of hard and soft substratum types in the study area.

Soft-sediment substrata

The composition and distribution of sediments on the south-eastern Australian shelf results from processes occurring in both modern and ancient times. The distribution of carbonates and their increase with depth illustrate the continent's history of tectonic stability and relative aridity since the Oligocene (26 million years ago). Australia is a dry continent with low-relief (Blom and Alsop 1988), resulting in low rates of sedimentation and the characteristic genesis of glauconites (Kelly and Webb 1996). Stable carbon ($\delta^{13}C$) concentrations in the sediment were in the range expected from material obtained from temperate marine phytoplankton (Fry and Sherr 1984), indicating little transport on to the shelf from terrestrial or nearshore sources (Bax *et al.* 2001). Glauconites are typically formed in low oxygen environments, often associated with high primary productivity. The source of this productivity may be deep upwelling over the shelf break.

Carbonates in outer-shelf sands, south of 24°S, are formed primarily from Foraminifera, Mollusca, Bryozoa and calcareous red algae, while between 38° and 44°S, bryozoans become the dominant constituent of outer-shelf sands, commonly exceeding 60% of overall composition (Marshall and Davies 1978). The abundance of bryozoans on the outer-shelf in these southern latitudes is possibly related to the upwelling of nutrient-rich, Antarctic intermediate water along the southern shelf (Wass *et al.* 1970). Marshall and Davies (1978) describe 'forests of living Bryozoa' on the outer-shelf that continually add to the surrounding relict sediments. It is this deep upwelling of nutrient-rich slope water that contributes to the productive habitat and fishing grounds along the shelf-break, and especially at canyon heads in this area (Bax *et al.* 2001).

The south-eastern Australian continental shelf is a moderate to high-energy, wave-dominated environment (Morrow and Jones 1988). The rippled, inner-shelf sediments show the influence of water currents, waves and surface swell. Fine sediments settle out locally in shallow sheltered areas (e.g. off Wilsons Promontory and Disaster Bay) and, more generally, at greater depths where the waves do not penetrate. Pollen from recent plant introductions, for example Monterey pine (*Pinus radiata*) and agricultural weeds, is found in outer-shelf muds, confirming their recent origins (Jones and Davies 1983).

Physical factors that cause changes in sediment size and bottom ripples with depth also affect the distribution of invertebrates and fish. Both show distinct trends with depth and with the presence of deep upwelled water and nutrients at the heads of the Bass Strait canyon (Bax and Williams 2000; Williams and Bax 2001). The distribution of biological communities is intimately related to the distribution of bottom sediments, due either to biological communities being influenced by sediment composition, or to similar physical processes affecting both their distribution of biological communities and sediments (Snelgrove and Butman 1994). Factors that affect the sediment distribution or the microhabitat features (wave-induced ripples in shallower water, bioturbation in deeper or more sheltered water) will also affect the distribution of biological communities dependent on them. Various taxa associate with biogenic depressions, shells, burrows, sand wave crests and amphipod tubes (Auster *et al.* 1991, 1995, 1997).

Consolidated rock/reef substrata

The distribution of biological communities in this area is also affected by the presence of hard-grounds, predominantly limestone reefs and outcrops of sandstone and granite (Williams and Bax 2001). Fossiliferous

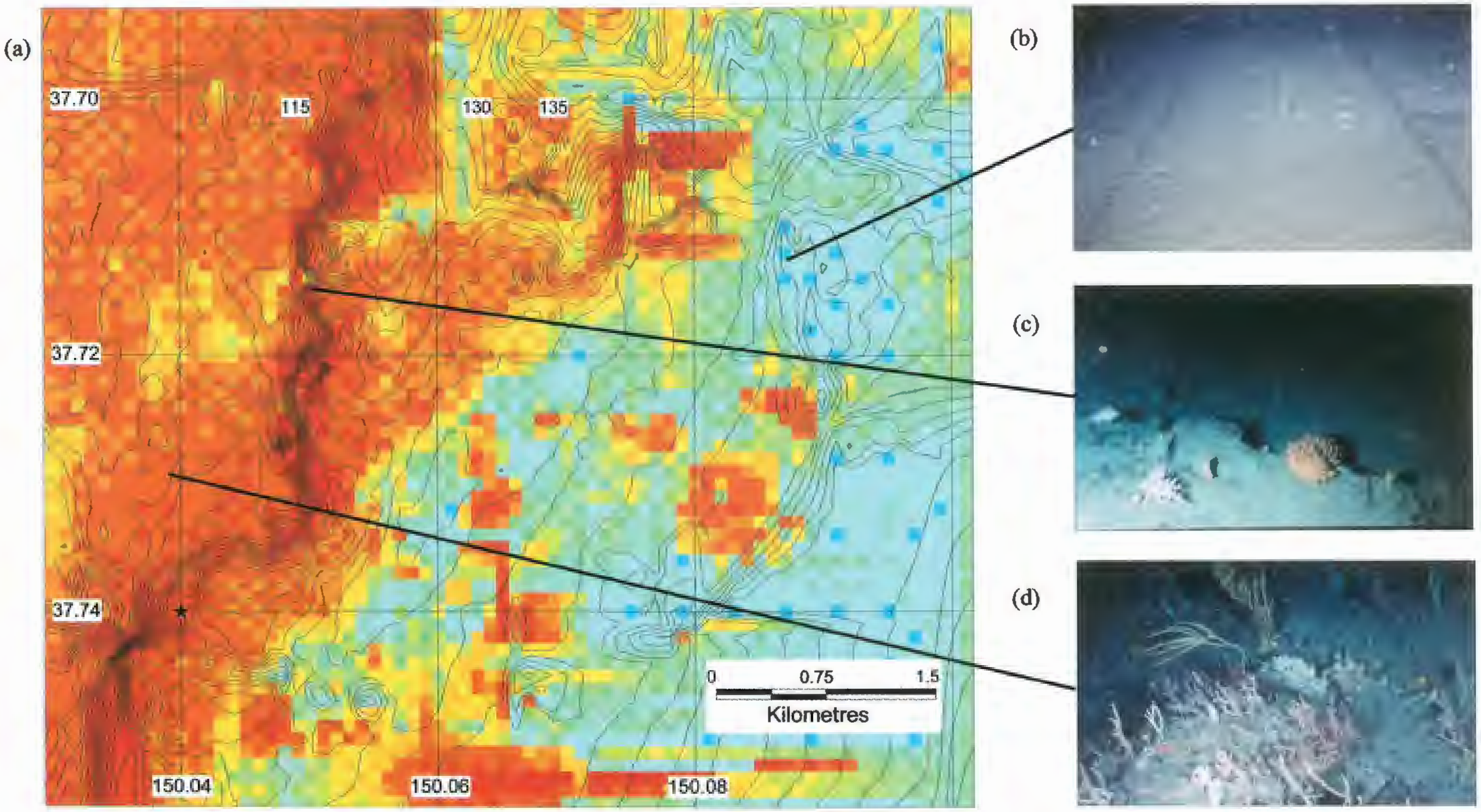


Plate III. Example of mesohabitat mapping: Gabo Reef showing *(a)* location and bathymetry (m) overlaid on a mesoscale habitat map [interpolated acoustic index of bottom roughness; most rough (red) to least rough (blue)]. Images indicate mesohabitat types and locations: *(b)* soft, sediment adjacent to reef; *(c)* hard, reef edge; and *(d)* rough, reef platform.

limestone is composed of the hard, carbonate skeletons of dead animals, such as bivalve and bryozoan clasts. The skeletal elements are cemented together by a fine-grained calcareous matrix. The presence of glauconite (green silicate material and pyrites) and lack of burial or compaction features indicates a relatively slow rate of sedimentation and long periods of exposure to marine waters that allowed the precipitation of an even sheet of limestone. Bernecker *et al.* (1997) indicated that similar fossiliferous limestones are currently being deposited on much of the Gippsland Basin continental shelf. Local heterogeneities stem from variation in a number of factors including skeletal assemblages, currents, cementation, and burial rates. In addition to these 'modern' reefs, it is also likely that 'ancient' limestone crops out through unconsolidated sediments. However, we were not able to differentiate between the two forms from the limited number of rocks sampled or from photographic images.

Coarse-grained sandstone, consisting largely of quartz grains, crops out as tabular slabs from soft sediments off the Gippsland coastline. Again, the presence of glauconite supports a marine origin and slow sedimentation rate, whereas the lack of stylolites or other compaction features indicates lack of burial. Combined, these properties suggest that this rock formed in a high-energy, coastal plain environment, a scenario consistent with Bernecker *et al.* (1997). The overall morphology of sandstone outcrops (occurring together with fossiliferous limestone) — elongate, low-relief and parallel to the present-day Gippsland coastline — suggests that the rocks were formed in sand bodies along palaeo-coastlines.

The composition and characteristics of the hard-grounds vary based on their geologic origin and history. For example, present sea levels, considered to have prevailed for some 6000 years, are at least 67 m higher than before the last glacial regression, when Bass Basin (adjacent to the Gippsland coast) was a shallow marine embayment (Blom and Alsop 1988); recent swath sonar mapping of the area suggests an earlier coastline at 140–150 m depth (Rudy Kloser, CSIRO Marine Research, Australia, unpublished). Rock outcrops that were exposed during the last ice age will have been weathered and be relatively fragile compared with outcrops of similar geologic history that remained submerged. The fragility of the rock outcrops will affect their resilience to damage by fishing. Many of these hard-grounds serve to aggregate economically valuable fish species and are targeted by commercial fishers with trawls, setnets and traps.

The modern sedimentary processes and the geologic history of sediments and rock outcrops briefly described here have led to a mosaic of seabed habitats on the continental shelf off south-eastern Australia. Distinct features in this mosaic, such as limestone reefs, operating at different scales, are differentially exploited by biological communities and fishers. The distribution of fish with habitat is a multiscale pattern where the scale is dependent on the species and processes being considered (Garcia-Charton and Perez-Ruzafa 1999). However, appropriate spatial scales need to be defined if we are to effectively manage use of the seabed habitat in this area. Here we suggest three levels at which seabed could be mapped for management purposes by using currently available information and technology. We also attempt to answer the question of which seabed habitats are particularly vulnerable to disturbance.

Provincial-scale mapping, providing the context for interpreting seabed habitat, its use and vulnerability

Seabed habitat is just one factor influencing the distribution of biological communities. The distribution of fish and invertebrate communities in this and other areas is also correlated with latitude, depth and hydrology (e.g. Gray and Otway 1994; Perry and Smith 1994; Langton *et al.* 1995; Roberts and Davis 1996; Karakassis and Eleftheriou 1997; Bax and Williams 2000). At the largest scale, our study area is a faunal transition zone, or biotone, containing cool and warm temperate faunas; a major cross-shelf faunal disjunction occurs near Cape Howe, coinciding with an overlap of temperate and subtropical currents (IMCRA 1998; Williams and Bax 2001).

Hydrology affects the distribution of biological communities at several spatial scales below the along-shore patterns described above (e.g. Lough *et al.* 1989; Genin *et al.* 1993; Gaertner *et al.* 1999). Waves of 1–3 m average height and strong currents (>50 cm s^{-1}) driven by westerly winds and gales penetrate to a depth of at least 60 m (Fandry 1983; Morrow and Jones 1988). The influence of these waves and currents decreases as water depth increases. Both invertebrate and fish communities in this area are correlated with depth and three communities can be distinguished (inner-shelf <40 m, outer-shelf 40–160 m, and shelf-break >160 m), although the overlap between invertebrate and fish communities is not exact (Bax and Williams 2000; Williams and Bax 2001). Many fish species extend over several of these fish communities, but for most of the abundant species, larger individuals are more abundant offshore in deeper water (Chen *et al.* 1997; Jordan 1997; Bax and Williams 2000).

At a local scale, hydrology can affect the composition of the communities present. In this region, deep upwelling at the Horseshoe Canyon head contributes to distinctive and rich faunas: the presence of continental slope fishes at unusually shallow depths and a sessile epifauna dominated by stalked crinoids. At Point Hicks, strong currents in shallow waters lead to a distinctive community of predominantly dorso-ventrally flattened fish (Williams and Bax 2001). The currents that influence biological communities also affect the deposition, resuspension and sorting of sediments. Thus the deep upwelling at the Horseshoe can be inferred from the fine, organically rich sediments in that area, whereas the strong currents at Point Hicks can be inferred from the high amplitude waves of coarse sand.

These factors – latitude, hydrology (at several scales) and depth – are correlated with the distribution of sediments, biological communities and different size classes of individual species. They provide the context for interpreting seabed habitat, its uses and vulnerability in this area. Superimposed on these larger-scale patterns are megascale seabed features.

Megascale mapping: an operational level for managing anthropogenic habitat use

Fishers' information on habitat, gained through their almost daily 'sampling' of the seafloor, was mapped at scales of 10s to 100s sq. km to produce a megascale map of seafloor types and primary fishing grounds (Plate II). The scale of this map is appropriate for scientists to understand the interaction of the fishers with the seascape (effort and catch), and to direct scientific sampling of habitats. Collaborating with fishers acknowledges their broad and often detailed knowledge of the seafloor, exemplified by their provision of 'place names' for maps (Neis 1995). The alternative to using fishers' information – megascale scientific mapping of the seafloor – is still being developed and would require considerably greater resources (Kloser *et al.* 2001).

Working with the fishers using the area is an effective way to develop management models that are fine-tuned to local conditions, implying that management of human activity may be most effective when it is done on local scales (Argady 1997). Fishers have a vested interest in ensuring that their local grounds remain productive. Existing physical refuges from fishing activity may play a major part in sustaining that productivity. In most cases, fisheries that have been sustained over long periods without resorting deliberately to large space or time closures, have had some natural or bioeconomic refuge that has protected large parts of the stock from fishing (Walters 1998). Productivity in the fishery is likely to decline if the hard-grounds that provide physical refuges are reduced over time (Beverton 1992; Walters and Juanes 1993; Thrush *et al.* 1998). The association of many taxa with structural habitat implies an increase in individual fitness that would be lost if the structural features were lost (Auster and Malatesta 1995). Furthermore, the role of structural habitat as a fish aggregating device (Williams and Bax 2001) indicates that its loss would reduce the efficiency with which fishers could catch the (previously) aggregating species.

Addition of geological and biological attributes to determine vulnerability of seabed habitat

Whereas some habitats may be vulnerable to a particular physical disturbance, others may not. Adding biological and geological information to the coarse scale fishers' map provides one way in which a habitat's vulnerability to physical disturbance can be defined. We define vulnerability here as the product of a habitat's resistance to modification from a particular source and its resilience, or the time taken for the habitat to resume its original ecosystem functions (or more conservatively its original condition) once the modifier is removed.

Benthic habitat in regularly disturbed areas (e.g. the surf zone) may be relatively invulnerable to physical disturbances that are less than those that occur naturally; the system will resume its original ecosystem functions after the next natural disturbance. Conversely, even small physical modification to habitats at greater depths than those where storm events penetrate may persist over long periods of time, making those habitats more vulnerable. The time to recovery of ecosystem functions following modification will vary depending on the type of disturbance. It will be most rapid for sediment redistribution in high energy environments, less rapid for the biota dependent on those sediments, on the order of decades or centuries for slow-growing biota (e.g. deep sea corals), and on the order of millenia for structural habitat required by sessile biota for anchorage. Thus, although weathered limestone reefs may be more able to resist physical disturbance than unconsolidated sediments, they may be more vulnerable to a particular physical disturbance because once modified they are unlikely to recover in the human time frame, i.e. they have low resilience.

This concept of vulnerability is shown diagrammatically (Fig. 5) and below we apply it to the megascale features observed in our surveys.

Effects of fishing on the structure and stability of sediment flats in this predominantly high-energy, current-swept shelf environment are unknown but may not always cause long-term modification. Storm-related waves reach to at least 60 m depth in this area (Fandry 1983; Morrow and Jones 1988), suggesting that unconsolidated substrata in exposed areas at less than 60 m will be naturally disturbed on a regular basis. In sheltered areas and at depths greater than 60 m, where storm-related waves do not penetrate, unconsolidated sediments are not as regularly disturbed (except in some areas with high current flow, e.g. Bass Strait canyon down to at least 850 m; Williams, personal observation), biological activity (bioturbation) is higher, and fishing is more likely to have long-lasting effects. Unfortunately, because most unconsolidated sediment flats have been fished for decades, effects are difficult to evaluate.

Fishers report smothering of upper-slope reefs by current-borne sediment disturbed on the shelf. This is consistent with sediment resuspension reported as a result of trawling in other areas of the world, for example the Gulf of Maine, where resuspended sediments and infauna were found 25 m off the bottom (Pilskaln *et al.* 1998). Periodic burial of reefs may also occur naturally in hydrodynamically energetic areas, making it difficult to distinguish fishing effects from natural events. Resuspended bottom material was an order of magnitude higher in a basin of the Gulf of Maine strongly influenced by currents from the Bay of Fundy than in the area affected by trawling (Pilskaln *et al.* 1998 and personal communication).

Rock and sediment samples showed that 'hard-ground' habitats are fossiliferous limestone reefs formed of bivalve and bryozoan clasts, sediments consolidated by reef-forming bryozoans, indurated (cemented) sediments, and outcrops of granite basement rocks and sandstone bedrock (Fig. 3). Their resistance to deleterious modification by fishing gears is highly variable and determined by the degree of hardness, degree of weathering, relief, areal extent and spatial integrity (Auster 1998). Recovery of hard-ground habitats is so long term as to be effectively zero, causing any hard-ground habitats with low resistance to modification to be classified as highly vulnerable.

Some of the most vulnerable habitats are shelf-break bryozoan reefs (e.g. those of the Flower Patch, Plate II*i*) that are soft and lightly attached, have minimal vertical relief (<30 cm) and exist as small patches (1–10s of sq. m). Bryozoan reefs may be completely removed by fishing gear, but nothing is known about their recovery times in this area. Tasman Bay in New Zealand was closed to commercial fishing to protect bryozoan reefs that are important to the productivity of economically important fish stocks (Bradstock and Gordon 1983).

Many inner-shelf fossiliferous limestone and sandstone reefs that were exposed during the last low sea level stand are also vulnerable because they are relatively soft, highly weathered, have low relief (<2 m) and exist in isolation or as patchworks intersected by gutters, e.g. Broken Reef. In relation to trawling this means their physical structure can be damaged by tow wires (sawing) or removed by nets. Their spatial structure, often consisting of multiple reef patches, is amenable to 'opening up' or subdivision by trawl tows. Having only low-relief means that areas may be towed over by using robust ground gear fitted with rollers or bobbins or by 'environmentally friendly' trawls designed for light bottom contact. In some instances 'environmentally friendly' may be a dangerous misnomer. The area is reported as being progressively opened up to trawling, although whether this is due to local sediment movement or removal of structural habitat by fishing activity cannot be ascertained. It is possible that carefully targeted preservation or, in other cases, controlled opening up of

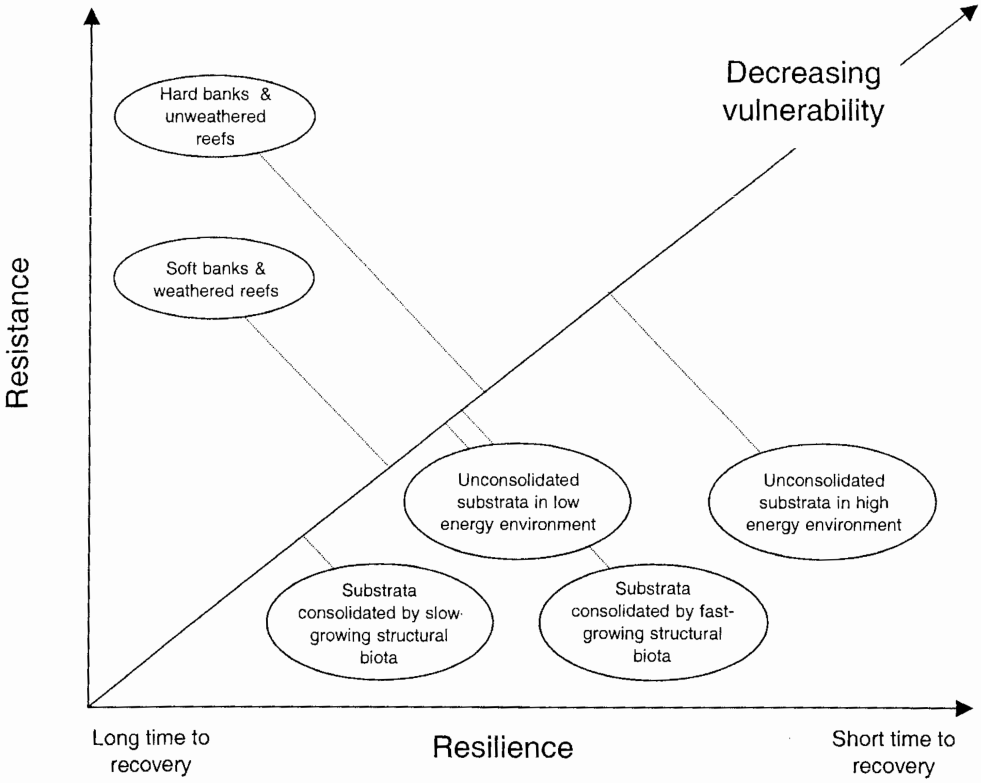


Fig. 5. Vulnerability of generalized substratum types based on their resistance to physical modification and their resilience once modified.

these habitats has the potential to enhance fishery productivity. However, once eroded these low relief reefs may never recover. Current activities will need to be monitored at much finer detail than is the case at present if we are to understand the effect of fishing on these vulnerable habitats.

Most resistant and therefore least vulnerable are highly cemented, deep, high-relief (up to 10 m high), large and undivided fossiliferous limestone reefs such as Gabo Reef, and granite outcrops. Concentrated fishing effort using mobile gear (trawls) occurs offshore of this largely resistant reef. Contiguous with and to the north of Gabo Reef, fishing effort is concentrated on narrow gutters (e.g. Big Gutter) between (and sometimes over) low-relief (<1 m) slabs of fossiliferous reef. These gutters have been fished for many years with no reported decline in productivity (Bax and Williams 2000). It is possible that opening up of hard-ground, especially extensive areas such as western Bass Strait, may increase fishery productivity. However, it is too early to say to what extent hard-ground areas can be opened up without reducing overall fishery productivity. Again, there is much to be learned through monitoring current activities.

A habitat's vulnerability and an effect's intensity determine the magnitude of effect once a particular event has occurred. However, the likelihood that a habitat will be affected by a particular event is the product of that magnitude and its probability of occurrence. Knowledge of both is required to manage human effects on seabed habitat. In our study area, the probability of effect is highest for habitats that are prospective fishing areas. Such areas typically have: a greater abundance, or larger individuals, of commercially fished species; a geomorphology that provides low risk of fouling ground-gears (soft substratum with low relief and a lack of overhangs); and a patchy distribution that is amenable to subdivision by trawling. This could provide a third dimension in Fig. 5, but is beyond the scope of this paper.

Effects of fishing gear on seabed habitats can be reduced by reducing the magnitude of effect (gear modification), or reducing the probability of effect (effort management). Knowledge of both is required to make the most appropriate management intervention for a particular fishery or habitat.

Mesoscale mapping: monitoring effects and recovery

Although megascale maps (showing features of 1 to 10s of km) can be used to establish habitat values and therefore could be used to manage habitat use, their scale is too coarse for monitoring purposes. Monitoring, and therefore mapping, at the mesoscale (showing features of 10 m to km) is necessary because the high spatial variability at larger scales obscures effects of habitat use or management intervention. Theoretical and empirical studies indicate that mesoscale heterogeneity is an important component of ecological systems, with implications for the maintenance of diversity and stability at population, community and ecosystem levels (Walters and Juanes 1993; Syms 1995; With and Crist 1995; Thrush *et al.* 1998; Auster and Langton 1999). With the advent of satellite-based navigation systems, fishers also operate at the mesoscale. If fishers are not to be excluded from some of the most productive fishing grounds, then management of fishing effort will also need to account for mesoscale habitat variability.

Mesoscale mapping requires considerable scientific effort, which is why it would be impossible, given currently available technology, to apply it over large areas. In this study we used acoustics (Kloser *et al.* 2001), video on a towed camera platform (Barker *et al.* 1999), and a benthic sled (Bax and Williams 2000) to identify and map the mesoscale features at which fishers target their effort. All three sampling methods are important for cross-validation and interpolation of habitat details. Acoustic methods can provide distributions of habitat types at this resolution but it requires representative *in situ* sampling to determine what these habitat types are. The examples of focussed megahabitat sites provided in this paper illustrate the mesohabitat variability that can be expected at this scale, and therefore indicate the scale at which monitoring would need to occur to distinguish natural variability from change.

We have provided results from mapping the south-eastern Australian shelf at three scales. The maps from each scale provide information, but it is the three scales together that provide a better understanding of seabed habitat in this area. A central feature of our sampling strategy was using existing information to prestratify sampling effort. Intensive exchanges with knowledgeable fishers gave us a coarse-scale map of the major seabed features in this area: sediment flats, low-relief reef, high-relief reef and the fauna associated with them. We could not have collected the same information with random, stratified or regular scientific surveys, given the resources available, because the major seabed features in this area are irregular and often small. Many of the features known to fishers from years of searching would not have been found. The scale of the problem is illustrated by the time it took to map the megahabitat defined for each major feature, 2–3 days of ship time, although it included acoustics, photographic work, sediment sampling, fish sampling and invertebrate sampling. The initial provincial scale survey of the area provided information on the general hydrology and geology of the area and the context with which to explain differences in (fish) community composition between different megahabitats. It also provided the information from which to infer vulnerability of different megahabitats, and the necessary information with which to extrapolate our information to unsurveyed areas.

Mapping seabed habitat in the South East Fishery has the capacity to provide a basis for sound spatial management of fishing effort in this area. The approach we have used has the advantage of amalgamating scientific and fishers' information. But before spatial management of fishing effort can progress, it will be necessary to determine what the management goals are; maximizing sustainable fisheries production, conservation of habitat, conservation of biodiversity, and conservation of particularly vulnerable taxa are just a few of the possible options. In our conversations with fishers, some individuals have expressed concern at opening up new fishing grounds, in particular well fished areas, because it may remove the habitat necessary to sustain the targeted species. In other lightly fished areas, opening up of new grounds may be the only way to effectively harvest previously underutilized species. Different fishers using different gear types (trawls, traps, setnets, droplines and longlines) will have different requirements for habitat use to maximize their fishing efficiency. Their different, and sometimes conflicting, requirements will need to be considered alongside conservation goals once they are determined. We have provided a hierarchical approach to mapping seabed habitat in this area. It is one of the first steps in building a common framework of knowledge on which future management options can be explored for mutual benefit.

Acknowledgments

Many people contributed to this project. Karen Gowlett-Holmes provided invaluable invertebrate expertise, designing the invertebrate sampling protocols and interpreting the videos. Bruce Barker developed the camera systems, interpreted videos and produced many of the figures. Rudy Kloser developed and operated the acoustic equipment. Tim Ryan processed and quality checked the acoustic data. Peter Winefield (University of Tasmania) analysed the rock samples and, with Rob Reid, provided a geological intepretation of the area. Stevie Davenport collected and analysed the stable isotope data. Fishers from the ports of Lakes Entrance and Eden were generous with their time and information in naming and mapping major features in the area. The master, mates and crew of the *Southern Surveyor* deployed gear and obtained the samples in all weather. Jessica Farley and Vince Lyne (CSIRO) improved an earlier draught of the paper. The paper was further improved following comments from Gary Greene of Moss Landing. The project was supported by Grant 94/040 from the Fisheries Research and Development Corporation.

References

Argady, T. S. (1997). 'Marine Protected Areas and Ocean Conservation.' (R. G. Landes Co.: Austin, TX.)

Auster, P. J. (1998). A conceptual model of the impacts of fishing gear on the integrity of fish habitats. *Conservation Biology* **12**, 1–6.

Auster, P. J., and Langton, R. W. (1999). The effects of fishing on fish habitat. *American Fisheries Society Symposium* **22**, 150–87.

Auster, P. J., and Malatesta, R. J. (1995). Assessing the role of non-extractive reserves for enhancing harvested populations in temperate and boreal marine systems. In 'Marine Protected Areas and Sustainable Fisheries'. (Eds N. L. Shackell and J. H. M. Wilson.) pp. 92–89. (Science and Management of Protected Areas Association: Wolfville, NS, Canada.)

Auster, P. J., Malatesta, R. J., LaRosa, S. C., Cooper, R. A., and Stewart, L. L. (1991). Microhabitat utilization by the megafaunal assemblage at a low relief outer continental shelf site – Middle Atlantic Bight, USA. *Journal of Northwest Atlantic Fisheries Science* **11**, 59–69.

Auster, P. J., Malatesta, R. J., and LaRosa, S. C. (1995). Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. *Marine Ecology Progress Series* **127**, 77–85.

Auster, P. J., Malatesta, R. J., and Donaldson, C. L. S. (1997). Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. *Environmental Biology of Fishes* **50**, 195–200.

Barker, B. A. J., Helmond, I., Bax, N. J.,Williams, A., Davenport, S., and Wadley, V. A. (1999) A vessel-towed camera platform for surveying seafloor habitats of the continental shelf. *Continental Shelf Research* **19**, 1161–70.

Bax, N. J., and Williams, A. (Eds) (2000). Habitat and fisheries productivity in the South East Fishery. Final report to FRDC Project 94/040, CSIRO Marine Research, Hobart, Tasmania, Australia, 495 pp.

Bax, N. J., Burford, M., Clementson, L., and Davenport, S. (2001). Phytoplankton blooms and production sources on the south-east Australian continental shelf. *Marine and Freshwater Research* **52**, 451–62.

Bax, N., Williams, A., Davenport, S., and Bulman, C. (1999). Managing the ecosystem by leverage points: a model for a multispecies fishery. In 'Ecosystem Approaches for Fisheries Management'. pp. 283–303. (Alaska Sea Grant College Program, AK-SG-99-01)

Bernecker, T., Partridge, A. D., and Webb, J. A. (1997). Mid–late tertiary deep-water temperate carbonate deposition, offshore Gippsland Basin, southeastern Australia. In 'Cool-water Carbonates'. (Eds N. P. James and J. Clarke.) pp. 221–36. (SEPM Special Publication 56, Tulsa, OK.)

Beverton, R. J. H. (1992). Fish resources; threats and protection. *Netherlands Journal of Zoology* **42**, 139–75.

Blom, W. M., and Alsop, D. B. (1988). Carbonate mud sedimentation on a temperate shelf: Bass Basin, southeastern Australia. *Sedimentary Geology* **60**, 269–80.

Bradstock, M., and Gordon, D. P. (1983). Coral-like bryozoan growths in Tasman bay, and their protection to conserve commercial fish stocks. *New Zealand Journal Marine Freshwater Research* **17**, 159–63.

Chen, Y., Liggins, G. W. Graham, K. J., and Kennelly, S. J. (1997). Modelling the length-dependent offshore distribution of redfish, *Centroberyx affinis*. *Fisheries Research* **29**, 39–54.

Chivers, R. C., Emerson, N., and Burns, D. R. (1990). New acoustic processing for underway surveying. *Hydrographic Journal* **56**, 9–17.

Davies, P. J. (1979). Marine geology of the continental shelf off southeast Australia. Department of National Resources, Bureau of Mineral Resources, Geology and Geophysics Bulletin No. 195. (Australian Government Publishing Service: Canberra.)

Edwards, R. J. (1990). Upwelling could hold clues to fish patterns. *Australian Fisheries* **49**, 18–20.

Fandry, C. B. (1983). Model for the three-dimensional structure of wind-driven and tidal circulation in Bass Strait. *Australian Journal of Marine and Freshwater Research* **34**, 121–41.

Fleming, N. C., and Roberts, D. G. (1973). Tectono-eustatic changes in sea level and seafloor spreading. *Nature* **243**, 19–22.

Folk, R. L. (1974). 'Petrology of Sedimentary Rocks.' (Hemphill, TX.)

Fry, B., and Sherr, E. B. (1984). $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* **27**, 13–47.

Gaertner, J. C., Mazouni, N., Sabatier, R., and Millet, B. (1999) Spatial structure and habitat associations of demersal assemblages in the Gulf of Lions: a multicompartmental approach. *Marine Biology* **135**, 199–208.

Garcia-Charton, J. A., and Perez-Ruzafa, A. (1999). Ecological heterogeneity and the evaluation of the effects of marine reserves. *Fisheries Research* **42**, 1–20.

Genin, A., Greene, C., Haury, L., Wiebe, P., Gal, G., Kaartvedt, S., Meir, E., Fey, C., and Dawson, J. (1993). Zooplankton patch dynamics: daily gap formation over abrupt topography. *Deep Sea Research* **41**, 941–51.

Gray, C. A., and Otway, N. M. (1994). Spatial and temporal difference in assemblages of demersal fishes on the inner continental shelf off Sydney, south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **45**, 665–76

Greene, H. G., Yoklavich, M. M., Sullivan, D., and Cailliet, G. M. (1994). A geophysical approach to classifying marine benthic habitats: Monterey Bay as a model. In 'Applications of Side-Scan Sonar and Laser-Line Systems in Fisheries Research'. pp. 15–30. (Alaska Department Fish and Game: Juneau.)

Greene, H. G., Yoklavich, M. M., Starr, R. M., O'Connell, V. E., Wakefield, W. W., Sullivan, D. E., McRea, J. E. Jr, and Cailliet, G. M. (1999). A classification scheme for deep seafloor habitats. *Oceanologica Acta* **22**, 663–78.

Holling, C. S. (1992). Cross-scale morphology, geometry and dynamics of ecosystems. *Ecological Monographs* **62**, 447–502.

IMCRA (1998). Interim Marine and Coastal Regionalisation for Australia: an ecosystem-based classification for marine and coastal environments. Commonwealth of Australia, 104 pp.

Jones, H. A., and Davies, P. J. (1983). Superficial sediments of the Tasmanian continental shelf and part of Bass Strait. Department of Resources and Energy, Bureau of Mineral Resources, Geology and Geophysics Bulletin No. 218. (Australian Government Publishing Service: Canberra.)

Jordan, A. R. (1997). Demersal trawl surveys of the continental shelf of southern and eastern Tasmania 1993–95. Department of Primary Industries and Fisheries, Tasmania, Technical Report No. 50, 148 pp.

Karakassis, I., and Eleftheriou, A. (1997). The continental shelf of Crete: structure of macrobenthic communities. *Marine Ecology Progress Series* **160**, 185–96.

Kelly, J., and Webb, J. A. (1996). The genesis of glaucony in the Jan Juac formation, Torquay Basin, southeastern Australia. 13th Australian Geological Convention Abstract No. 49, Canberra.

Klaer, N. L. (2001). Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. *Marine and Freshwater Research* 52, 399–410.

Kloser, R. J., Bax, N. J., Ryan, T., Williams, A., and Barker, B. A. (2001). Remote sensing of seabed types in the Australian South East Fishery; development and application of normal incident acoustic techniques and associated 'ground truthing'. *Marine and Freshwater Research* **52**, 475–89.

Kolasa, J. (1989). Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* **70**, 36–47.

Langton, R. W., Auster, P. J., and Schneider, D. C. (1995). A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. *Reviews in Fisheries Science* **3**, 201–29

Larcombe, J. W. P., McLoughlin, K. J., and Tilzey, R. D. J. (2001). Trawl operations in the South East Fishery, Australia: spatial distribution and intensity. *Marine and Freshwater Research* **52**, 419–30.

Lough, R. G., Valentine, P. C., Potter, D. C., Auditore, P. J., Bolz, G. R., Nielson, J. D., and Perry, R. I. (1989) Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bauk. *Marine Ecology Progress Series* **56**, 1–12.

Marshall, J. F., and Davies, P. J. (1978). Skeletal carbonate variation on the continental shelf of eastern Australia. *BMR Journal of Australian Geology and Geophysics* **3**, 85–92.

McLean, R. F., Stoddart, D. R., Hopley, D., and Polach, H. (1978). Sea level change in the Holocene on the northern Great Barrier Reef. *Philosophical Transactions of the Royal Society London A* **291**, 167–86.

Morrow, R. A., and Jones, I. S. F. (1988). Sea floor drag coefficients – eastern Bass Strait. University of Sydney Ocean Sciences Institute Report No. 29. 7 pp.

Neis, B. (1995) Fishers' ecological knowledge and marine protected areas. In 'Marine Protected Areas and Sustainable Fisheries'. (Eds N. L. Shackell and J. H. M. Willison.) pp. 265–72. (Science and Management of Protected Areas Association: NS, Canada.)

Orlowski A. (1984). Application of multiple echoes energy measurements for evaluation of sea-bed type. *Oceanologia* **19**, 61–78.

Perry, I. P., and Smith, S. J. (1994). Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 589–602.

Pilskaln, C. H., Churchill, J. H., and Mayer, L. M. (1998). Resuspension of sediment by bottom trawling in the Gulf of Maine and potential geochemical consequences. *Conservation Biology* **12**,1–8.

Poiani, K. A., Richter, B. D., Anderson, M. G., and Richter, H. E. (2000). Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *Bioscience* **50**, 133–46.

Roberts, D. E., and Davis, A. R. (1996). Patterns in sponge (Porifera) assemblages on temperate coastal reefs off Sydney, Australia. *Marine and Freshwater Research* **47**, 897–906.

Roff, J. C., and Taylor, M. E. (2000). National frameworks for marine conservation – a hierarchical geophysical approach. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**, 209–23.

Rogers, S. I., Kaiser, M. J., and Jennings, S. (1998). Ecosystem effects of demersal fishing: a European perspective. In 'Effects of Fishing Gear on the Sea Floor of New England'. (Eds E. M. Dorsey and J. Pederson.) pp. 68–79. (MIT SeaGrant Publication 98–4.)

Sainsbury, K. J., Campbell, R. A., Lindholm, R., and Whitelaw, A. W. (1997) Experimental management of an Australian multispecies fishery: examining the possibility of trawl induced habitat modification. In 'Global Trends in Fisheries Management'. (Eds E. K. Pikitch, D. D. Huppert and M. P. Sissenwine.) pp. 107–12. (American Fisheries Society: Bethesda, MD.)

Schwinghammer, P., Guigne, J.-Y., and Siu, W. C. (1996). Quantifying the impact of trawling on benthic habitat using high resolution acoustics and chaos theory. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 288–96.

Senge, P. (1990). The Fifth Discipline: the Art and Practice of the Learning Organization. (Doubleday/Currency: New York.)

Simberloff, D. (1998). Flagships, umbrellas and keystones: is single-species management passé in the landscape era? *Biological Conservation* **83**, 2247–57.

Snelgrove, P. V. R., and Butman, C. A. (1994). Animal–sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology: an Annual Review* **32**, 111–77.

Syms, C. (1995). Multi-scale analysis of habitat association in a guild of blennoid fishes. *Marine Ecology Progress Series* **125**, 31–43.

Tilzey, R. D. J. (Ed.) (1999). The South East Fishery 1998. [Fishery Assessment Report compiled by the South East Fishery Assessment Group.] (Australian Fisheries Management Authority: Canberra.)

Thrush, S. F., Hewitt, J. E., Cummings, V. J., Dayton, P. K., Cryer, M., Turner, S. J., Furnell, G. A., Budo, R. G., Milburn, C. J., and Wilkinson, M. R. (1998). Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecological Applications* **8**, 866–79.

US Magnuson–Stevens Fishery Conservation and Management Act (1996). Public Law 94–265. As amended through October 11, 1996.

Walters, C. (1998). Designing fisheries management systems that do not depend upon accurate stock assessment. In 'Reinventing Fisheries Management'. (Eds T. J. Pitcher, P. J. B. Hart and D. Pauly.) pp. 279–88. (Kluwer Academic: London.)

Walters, C. J., and Juanes, F. (1993). Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2058–70.

Wass, R. E., Conolly, J. R., and MacIntyre, R. J. (1970). Bryozoan carbonate sand continuous along southern Australia. *Marine Geology* **9**, 63–73.

Watling, L., and Norse, E. A. (1998). Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conservation Biology* **12**, 1180–97.

Williams, A., and Bax, N. J. (2001). Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52**, 513–36.

With, K. A., and Crist, T. O. (1995). Critical thresholds in species' responses to landscape structure. *Ecology* **76**, 2446–59.

Yaffee, S. L. (1999). Three faces of ecosystem management. *Conservation Biology* **13**, 713–25.

Manuscript received 4 January 2000; revised and accepted 15 November 2000

Mar. Freshwater Res., 2001, **52**, 513–36

Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf

Alan Williams and Nicholas J. Bax

CSIRO Marine Research, PO Box 1538, Hobart, Tas. 7001, Australia

Abstract. A multi-scale, multi-gear survey identified the spatial structure and compositions of fish communities from a range of seabed types on the south-eastern Australian continental shelf (25 m to ~200 m depth). Most communities are species-rich and contain many shared species. Multivariate analysis of distributions of 201 fishes showed communities to be correlated with depth, latitude and seabed type; correlation with hydrodynamic climate is suggested by patterns in morphology. Depth-related patterns occurred on soft-sediment and hard substrata; strong latitudinal (south-west/north-east) patterns identify the area as a faunal transition zone with a major faunal disjunction extending across the shelf. Community patterns were overlaid on distributions of substrata to produce a biophysical map. This mapping process is discussed in the context of spatial management: the ecologically significant scale at which to map habitat features and definition of management units for ecosystem-based management. A hierarchy of scaled ecological units is being developed for Australia's National Representative System of Marine Protected Areas (NRSMPA); given the scope of the NRSMPA initiative, surrogate measures of community structure will be required. Maps of substrata and topography, interpreted in the context of the broader depth and latitudinal community structure and as modified by hydrography, may provide one useful surrogate.

Introduction

Multispecies distribution data are being increasingly used to define bioregions, or 'ecological units' that can be used to support ecologically sustainable development of marine resources (e.g. Kerr and Ryder 1989; Langton *et al.* 1995; Greenstreet and Hall 1996; Walters and Bonfil 1999). Australia has developed a hierarchical bioregionalization of its marine environment at provincial (>1000s of km) and meso-scales (100s–1000s of km) to guide ecologically sustainable development of the variety of industries dependent on marine resources, and to guide the conservation and reservation of representative marine ecosystems (Environment Australia 1998; ANZECC TFMPA 1999*a*). This bioregionalization was based on the limits of distribution of a range of biota (primarily fishes) in conjunction with physical environmental attributes (IMCRA 1998). However, biological communities exist and are exploited at a much more local scale (metres to kilometres) and this has yet to be taken into account. The appropriate scale at which to understand and manage marine communities depends on the species and processes being considered (e.g. Auster 1988; Rose and Leggett 1990; Holling 1992; Auster and Malatesta 1995; Montevecchi and Myers 1995; With and Crist 1995). Local-scale effects are cumulative at the population level in marine fisheries (Langton *et al.* 1995) and therefore effective spatial management of marine resources will need to consider ecological patterns at both regional and local scales, integrating over these scales to provide a 'seascape' perspective (Garcia-Charton and Perez-Ruzafa 1999).

In this study we develop an approach to describe biophysical patterns at the local scale and then interpolate these patterns at the meso-scale, specifically the 'Twofold Shelf' meso-scale bioregion off south-eastern Australia (IMCRA 1998). The study is therefore complementary to the existing hierarchical bioregionalization leading to a full classification of fish communities in this area from a scale of metres to 1000s of kilometres.

The Twofold Shelf bioregion is an exposed and current-swept area (Fandry 1983; Morrow and Jones 1988) of some 32000 km^2 that extends to about 200 m depth on the south-eastern Australian continental shelf. It is the area of greatest fishing effort within one of the country's largest regional fisheries, the South East Fishery (SEF). The SEF is Australia's largest fishery for bottom- and near-bottom-dwelling finfishes (groundfishes), and the most important source for domestic markets. More than 100 species of teleosts and elasmobranchs form the commercial catch of the fishery (continental shelf and slope), although only 16 species or closely related species-groups managed by a system of catch-quotas make up the bulk of the landings (>80% by weight). The fishery has a long history in the Australian context, dating back to the early 1900s when trawling started (and see Tilzey and Rowling 2001). Today, the SEF fleet is made up of otter-board trawlers and Danish

10.1071/MF00017 1323-1650/01/040513

seiners (the 'trawl sector'), and demersal longliners, dropliners, mesh-netters and trappers (the 'non-trawl sector') (Caton *et al.* 1997). Research has tended to focus on single species stock assessments (Tilzey 1994). Until recently, there has been no attempt to investigate the ecosystem functions that support the productivity of the fishery. In particular, little was known about the spatial organization of habitats (substrata, biota and adjacent water column) or the ways in which the seabed has been used for fishing.

Our objectives in this study were three-fold. The first was to define the broad-scale community structure of demersal fish in the area by depth-stratified trawling. This was restricted to soft-sediment substrata, a limitation of using demersal trawl surveys in areas containing hard substrata (bedrocks, reefs and consolidated sediments) as well as soft-sediment substrata. Second, we planned to identify the association of fish communities with substratum type with a variety of gears (gill-net, traps and trawl) to ensure comprehensive coverage of all substratum types in the study area. Third, we planned to interpolate these specific examples of community–substratum association to the meso-scale by using the broad-scale community structure developed as the first objective and maps of substrata distribution developed with assistance from local fishers and refined by scientific sampling. We do not describe the derivation of the maps of substrata here as they are the subject of a companion paper in this issue (Bax and Williams 2001). Lastly, we discuss these results in relation to key issues in spatially based management of marine ecosystems, defining an ecologically significant scale at which to map habitat features (Auster and Malatesta 1995) and defining management units for ecosystem-based management (Langton *et al.* 1995).

Methods

Study area and sampling strategy

The study area was the Australian continental shelf adjacent to the coastline between Wilsons Promontory in eastern Victoria and Bermagui in southern NSW in the depth range of ~25–200 m (Fig. 1). Despite the long history of fishing in the area, there was little documented information on the types of seabed or their distributions to direct our survey design. Consequently, we used multiple gears in a two-phase sampling program with data from each component analysed separately.

First, a demersal trawl was used to sample soft-sediment substrata across a broad area. Samples were taken at five depth-stratified sites (25, 40, 80, 120, ~200 m depth) on each of seven cross-shelf transects (respectively, depths 1–5 on transects A–G in Fig. 1). Station positions included some surveyed a decade earlier (depths 1–3 on transects A–C; Moulton and Wankowski 1985). Samples were taken in four contrasting seasons: July 1993 (early winter), August 1994 (late winter), April 1996 (autumn) and November 1996 (spring).

In the second part of the survey, multiple gears—a gill-net, traps and the trawl—were used to sample six seabed areas (boxes in Fig. 1)

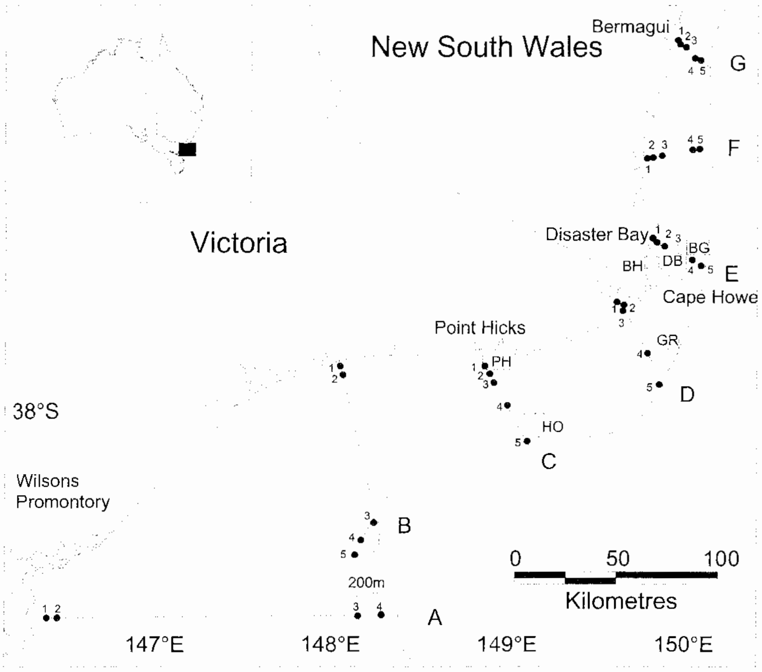


Fig. 1. Map of study area on the south-eastern Australian continental shelf showing the general positions of sampling sites. Soft-sediment substrata were sampled by trawl at depth-stratified sites (1–5) on each of seven cross-shelf transects (A–G), and different substrata sampled by multiple gears in six 'megahabitats' (boxes 1–6). (PH, Point Hicks; HO, Horseshoe; GR, Gabo Reef; BH, Black Head; DB, Disaster Bay; BG, Big Gutter).

comprising a range of substratum and morphological types including outcrops of bedrock, reef or consolidated sediments. These areas were termed 'megahabitats' (features that have dimensions from kilometres to tens of kilometres, and larger) and three sampling sites within them termed 'mesohabitats' (features having a size from tens of metres to a kilometre) following Greene *et al.* (1999). We used acoustic indices of seabed type (Bax *et al.* 1999*a*; Kloser *et al.* 2001) to discriminate the three mesohabitat sites, nominally 'rough' (R), 'hard' (H) and 'soft' (S). Megahabitats were chosen to represent the diversity of seabed types in the study area as assessed by acoustic information gathered during the first trawl survey and based on information generously provided by commercial fishers. Many megahabitats are also commercial fishing grounds.

Soft sediment and hard substrata were also sampled with cameras (Barker *et al.* 1999), and where possible a benthic sled and sediment sampler, to describe the physical and biotic structure of the seabed (Bax and Williams 2001). Details of the design and construction of the fishing gears are provided in Appendix 1.

Sample details

A summary of relevant samples is given in Appendices 2 and 3. Not all of the intended sites were sampled: soft-sediment Site A5 (~200 m) was too steep to trawl, and F1 (25 m) dangerously close to shore; Site D1 was missed in early winter because of extremely bad weather. All trawl samples analysed here were taken during the day (sunrise to one hour before sunset) except for 12 samples from the early-winter survey when nighttime trawling was necessitated by time constraints (short days and initial definition of trawlable grounds). We tested for a diel signal in species composition by using replicate trawls taken at one site (4 day and 4 night at C5 site) and the corresponding day samples from adjacent transects at the same depth (B5, D5) and adjacent depths (B4, C4, D4). Because multivariate analysis (below) showed no differentiation of day and night samples we retained the 12 nighttime trawls in the full data set. Day and night gill-net and trap samples were taken: all samples were used in a preliminary assessment of association of fishes with seabed type, but only daytime gill-net samples were used to analyse fish community structure.

The numbers and weights of each fish species were recorded for each sample. Taxonomic identifications were based primarily on Last and Stevens (1994) and Gomon *et al.* (1994) but also relied on a set of illustrated field identification sheets compiled during the study. Abundance data (weight of each species) were standardized to unit time to provide catch rates for gill-nets and traps (10-h soak for each six-panel net fleet or trap), and to area swept for trawls (by using wingspread measured by acoustic sensors for a 60 min tow at 3 kn). Trawl catches from each season were analysed separately. Gill-net catches from each set (two replicated fleets of panels per net) were averaged because they represent pseudo-replicated samples (Hurlbert 1984).

Data analysis

Multivariate analysis of species biomass distributions was used to examine fish community structure, with data from soft-sediment sites (131 samples) and megahabitats (34 samples) analysed separately. Modules of the PRIMER multivariate statistics package (Carr 1996) were used: CLUSTER (hierarchical agglomerative clustering) to form groups of samples (sites) based on between-sample similarities; MDS (non-metric multidimensional scaling) to display between-sample similarities in two-dimensional space; and ANOSIM to test for differences in similarities between seasonal groups. Arbitrary cut-off points in CLUSTER dendrograms were used to form groups in MDS plots. A similarity-of-percentages analysis (SIMPER; Clarke 1993) was used to identify the species that contributed most importantly to the similarities within groups of sites ('typical' species), and dissimilarities between groups of sites ('discriminating' species). The Bray–Curtis similarity index (Legendre and Legendre 1988) was used throughout. We analysed two subsets of standard samples (33 soft-sediment sites from August and 11 mesohabitat sites) to determine a transformation that appropriately weighted the relative contributions made by abundant and uncommon species. A fourth-root transformation, that de-emphasized the contribution of highly abundant species, consistently provided the lowest stress values in MDS plots and produced clear groupings for both data sets. It was used in all subsequent multivariate analyses. We used four properties of community composition to describe community structure: 'dominant' species (based on the geometric mean of biomass and total raw biomass); 'typical' and 'discriminating' species (from multivariate analysis); and 'restricted' species (those found in only one community).

In order to map biophysical regions, based on the association of distinct communities with distinct substrata, we had to determine an association between individual species and seabed type. A semi-quantitative 'degree of association' was defined by comparing the abundances of 61 species in gill-net catches ($n = 60$) and trap catches ($n = 22$) in samples from contrasting (soft-sediment and reef) substrata (taken during day and night). Only those species represented by ≥ 5 individuals were used. The numbers of individuals were standardized for the numbers of samples to calculate degree of association. Results from gill-net and trap catches were also cross-referenced to trawl samples from adjacent soft-sediments ($n = 10$). Three categories of association were used: 'strong' association (>95% of total individuals caught by gill-net and trap on one substratum type); 'distinct' (>70%); and association with 'both' (30–70%). Our confidence in the classification of each species was based on the agreement between gears, overall sample size (individuals), and agreement with the published literature if association was unclear (chiefly Kuiter 1993; Gomon *et al.* 1994). High confidence indicated a consistent association across gears and >100 individuals (unstandardized) in gill-net or trap. Medium confidence indicated a consistent association between gears but relatively small catches (>20 individuals in gill-net or trap), or, if catches were smaller, that literature accounts of seabed-type association were available for this region. Low confidence was assigned when agreement was inconclusive or few individuals (<20) were caught and no supporting literature was available. This analysis also enabled us to determine the utility of the different gears.

Results

Faunal composition and catches from megahabitats

The trawl caught most (113) of the total 143 species caught in megahabitat sampling despite not being used in rocky or reef mesohabitats; the gill-net caught 89 species, more than twice the number caught by trap (39). Only 24 species (17%) were caught by all three gears, whereas 64 species (45%) were caught by one only: 46 by trawl, 14 by gill-net and 4 by trap. There was a high overlap of species caught by the passive gears; 34 (87%) of trap-caught species were also caught by gill-net.

The passive gears had greater sampling utility than trawl as they were successfully deployed at all mesohabitats–including rugged and high relief (to 10 m) reefs. The trawl was deployed successfully on some hard substrata (mesohabitats with an intermediate acoustic index) but their contrast with adjacent soft-sediment mesohabitats was less than for gill-net or trap samples because the risk of gear damage forced us to be more conservative with trawl placement. The gill-net was more effective than traps as it caught greater quantities of fish, particularly in soft-sediment mesohabitats where trap catches were often small or zero. Moreover, it caught more species, including the great majority of those caught by trap. Not only were traps highly species-selective, but priority effects were evident. Although these were not assessed statistically, few smaller (prey) species were caught in the same trap as large predators, particularly *Conger verreauxi* (conger eel) and *Latris lineata* (striped trumpeter). Based on these findings, we used catches from all gears to examine the association between individual fish species and seabed type, but only gill-net data to examine fish community structure.

Associations between individual fish species and seabed type

In total, 61 species were caught in numbers of five or greater by gill-net or trap in mesohabitats that could be clearly identified as either soft-sediment or rock/reef. Overall, 38 species (61%) showed an association with one or other substratum type (Table 1). Among fishes from soft-sediments, the degree of association was strong (>95% individuals) in three species (5% of the total) and distinct (>70% individuals) in 14 species (23%). Among species on hard substrata, the degree of association was strong in 14 species (23%) and distinct in six species (10%). The remaining 24 species (39%) were caught in relatively large proportions (30–70%) on both seabed-types. Most determinations (85%) were made with a high or medium degree of confidence indicating that there was a good agreement in the catches of different gears based on sufficiently large catch sizes (Table 1).

Patterns of similarity among samples from soft-sediment substrata

A suite of 186 species caught by trawl during soft-sediment surveys (Appendix 4) was used to determine community structure. Multivariate analysis (classification and ordination) delineated seven fish communities based primarily on depth and latitude (south-west/north-east gradient). Consistent groups were formed by samples from inner-shelf depths 1 and 2 (25 and 40 m), outer-shelf depths 3 and 4 (80 and 120 m), and the shelf break depth 5 (~150–200 m) with very few 'cross-overs' between groups (Fig. 2*a–d*). South-westerly to north-easterly patterns (transects A–G) were also evident to varying degrees within depth-related groups in all seasons. Stress values (0.13–0.20) showed that between-sample similarity was adequately represented in two-dimensional MDS plots (Fig. 2*a–d*). Three outlying samples (late winter G2, spring G1 and G2) were represented by small catches (<100 kg unstandardized total weight). Because of the strong and consistent relationship with depth across seasons we re-aggregated the data to examine latitude and seasonal effects with the depth effect removed (Fig. 3).

Latitudinal patterns were distinct in all three depths groups (Fig. 3), although our analysis provided less contrast at the shelf break because transect A was not sampled there. Samples from transects A and B ('south-west') were most closely grouped, and were always distinct from samples from transects F and G ('north-east'). Samples from transects C, D and E ('central-region') grouped together, but formed a less distinct group on the outer shelf than on the inner shelf. Central samples variously combined with south-west and north-east groups, particularly samples from transect E (Disaster Bay) that were the most variable overall. north-east samples produced less defined groups than south-west samples, in part because of their similarities with transect E (Group 2, Fig. 3*a*; Group 3, Fig. 3*b*).

Only weak seasonal patterns were detected and these were not consistent across depth- or latitude-based groups. Winter samples tended to separate from spring and autumn at the shelf break (Fig. 3*c*), whereas a few early winter samples grouped separately on the outer shelf (Groups 2 and 5, Fig. 3*b*). Further ordination analysis of depth-groups within season repeated latitude patterns but failed to show a distinct or consistently different seasonal signal. There was a significant difference in the underlying species similarities between seasons with all samples compared (ANOSIM, Spearman correlation, $P < 0.001$) but this did not appear to be an important feature of community composition (see section on soft-sediment species below).

These patterns delineate seven fish communities from soft-sediment substrata across a broad region of the shelf. They are coded for comparative and mapping purposes as inner shelf south-west, central and north-east (ISW, IC and INE, respectively), outer shelf south-west and north-east (OSW and ONE, respectively) and shelf-break southern and northern (SBS and SBN, respectively) (and see communities 1–7 in Table 2).

Patterns of similarity among samples from different substrata in megahabitats

A suite of 87 species caught by gill-net during the megahabitat survey (Appendix 4) was used to determine community structure in adjacent soft-sediment and hard substratum types. Seven communities were delineated based primarily on depth, substratum-type and megahabitat (area) association. Depth-based grouping was strong with the delineation of inner shelf from outer shelf/shelf break mesohabitats at ~100 m (Fig. 4*a*). These two depth-related groups were sampled separately in different seasons but results from seasonal trawl sampling indicated that season did not strongly influence group formation. Stress levels for the MDS plots (<0.12) indicated that the data were adequately represented in two dimensions. Because the depth-related pattern was strong we also analysed the inner

Table 1. Associations of 61 fishes (no. individuals >5) with acoustically determined soft (soft-sediment) and rough (rock/reef) substrata on the south-eastern Australian continental shelf based on catches from gill-net (n = 60), trap (n = 22) and trawl (n = 10)

N, total (unstandardized) individuals caught by each gear; code, degree of association (SS, >95% on soft substrata; S, >70%; RR, >95% on rough substrata; R, >70%; B, 30–70% on either substratum type). The qualitative confidence of association is based on *(1)* the difference in relative abundance between substratum types *(2)* agreement between gears, and *(3)* the numbers of individuals caught; * indicates literature used to verify substratum association

Substratum association	No.	Species	Scientific name	Gill-net		Trap		Trawl	Confidence
				N	Code	*N*	Code	*N*	
Soft sediment, strong	1	Deepwater gurnard	*Lepidotrigla mulhalli*	31	SS	0		459	M
	2	Cucumberfish	*Chlorophthalmus nigripinnis*	19	SS	0		11468	H
	3	Yank flathead	*Platycephalus speculator*	5	SS	0		0	M*
Soft sediment, distinct	4	Piked spurdog	*Squalus megalops*	3300	S	76	B	301	H
	5	Jack mackerel	*Trachurus declivis*	3266	S	2	RR	5948	H
	6	Gummy shark	*Mustelus antarcticus*	266	S	4	SS	4	H
	7	Blue mackerel	*Scomber australasicus*	250	S	0		22	H
	8	Tiger flathead	*Neoplatycephalus richardsoni*	244	S	0		230	H
	9	Degens leatherjacket	*Thamnaconus degeni*	1	SS	138	S	21	H
	10	Southern sawshark	*Pristiophorus nudipinnis*	33	S	0		4	M
	11	Silver dory	*Cyttus australis*	13	B	15	SS	463	M
	12	Ruddy gurnard perch	*Neosebastes scorpaenoides*	9	S	3	SS	33	M*
	13	Peruvian jack mackerel	*Trachurus murphyi*	10	S	0		0	L
	14	School shark	*Galeorhinus galeus*	10	SS	0		2	L
	15	Southern rock cod	*Scorpaena papillosa*	6	B	0		3666	H*
	16	Blue grenadier	*Macruronus novaezelandiae*	6	SS	0		1	L
	17	Elephantfish	*Callorhinchus milii*	5	S	0		2	M*
Both	18	Jackass morwong	*Nemadactylus macropterus*	608	R	669	R	279	H
	19	Draughtboard shark	*Cephaloscyllium laticeps*	684	B	88	B	191	H
	20	Velvet leatherjacket	*Meuschenia scaber*	50	R	665	R	936	H
	21	Warehou	*Seriolella brama*	523	B	0		99	H
	22	Redbait	*Emmelichthys nitidus nitidus*	352	B	0		47	H
	23	Ocean perch	*Helicolenus percoides*	249	R	94	R	5398	H
	24	Barracouta	*Thyrsites atun*	326	B	0		54	H
	25	Orange-spotted catshark	*Asymbolus* sp D	231	B	15	R	83	H
	26	Redfish	*Centroberyx affinis*	228	B	0		1858	H
	27	Red cod	*Pseudophycis bachus*	40	B	123	R	23	H
	28	Pink Ling	*Genypterus blacodes*	112	R	5	RR	147	M
	29	Blue morwong	*Nemadactylus douglasi*	97	R	2	RR	421	H
	30	Port Jackson shark	*Heterodontus portusjacksoni*	79	B	1	SS	10	M
	31	Grey spotted catshark	*Asymbolus analis*	25	B	18	B	28	H
	32	Spotted trevalla	*Seriolella punctata*	39	RR	0		40	H*
	33	Sandpaper fish	*Paratrachichthys* sp 1	29	RR	0		25	M
	34	Rosy wrasse	*Pseudolabrus psittaculus*	6	B	23	RR	8	H*
	35	White trevally	*Pseudocaranx dentex*	28	B	0		24	M
	36	Sixspine leatherjacket	*Meuschenia freycineti*	7	RR	14	B	16	M
	37	Rusty carpetshark	*Parascyllium ferrugineum*	15	B	0		0	L
	38	Latchet	*Pterygotrigla polyommata*	12	B	0		25	L
	39	Eastern sawshark	*Pristiophorus* sp A	11	B	0		0	L
	40	Mosaic leatherjacket	*Eubalichthys mosaicus*	7	B	0		107	M*
	41	Common sawshark	*Pristiophorus cirratus*	5	R	0		0	L
Rock/ reef, distinct	42	Butterfly perch	*Caesioperca lepidoptera*	338	RR	13	RR	1314	H
	43	Eastern orange perch	*Lepidoperca pulchella*	47	R	172	RR	0	H
	44	Bearded rock cod	*Pseudophycis barbata*	8	RR	76	R	0	H
	45	Chinaman leatherjacket	*Nelusetta ayraudi*	1	RR	51	R	3	H
	46	Barber perch	*Caesioperca rasor*	3	RR	5	RR	0	M*
	47	Splendid perch	*Callanthias australis*	8	RR	0		10	M*
Rock/ reef, strong	48	Striped trumpeter	*Latris lineata*	19	RR	76	RR	0	H
	49	Mado	*Atypichthys strigatus*	2	RR	87	RR	0	H
	50	Bastard trumpeter	*Latridopsis forsteri*	65	RR	1	RR	1	H
	51	Common bullseye	*Pempheris multiradiata*	23	RR	0		0	M
	52	Maori wrasse	*Ophthalmolepis lineolata*	15	RR	8	RR	0	H*
	53	Longfin pike	*Dinolestes lewini*	19	RR	0		0	M*
	54	Largetooth beardie	*Lotella rhacinus*	2	RR	13	RR	0	H*
	55	Bluethroat wrasse	*Notolabrus tetricus*	7	RR	7	RR	0	H*
	56	Southern conger	*Conger verreauxi*	0		12	RR	0	M*
	57	Sergeant Baker	*Aulopus purpurissatus*	9	RR	1	RR	1	M*
	58	Swallowtail	*Centroberyx lineatus*	10	RR	0		0	M*
	59	Pigfish	*Bodianus* sp. 1	9	RR	1	RR	0	L
	60	Silver sweep	*Scorpis lineolata*	0		9	RR	0	M*
	61	Thresher shark	*Alopias vulpinus*	5	RR	0		0	L

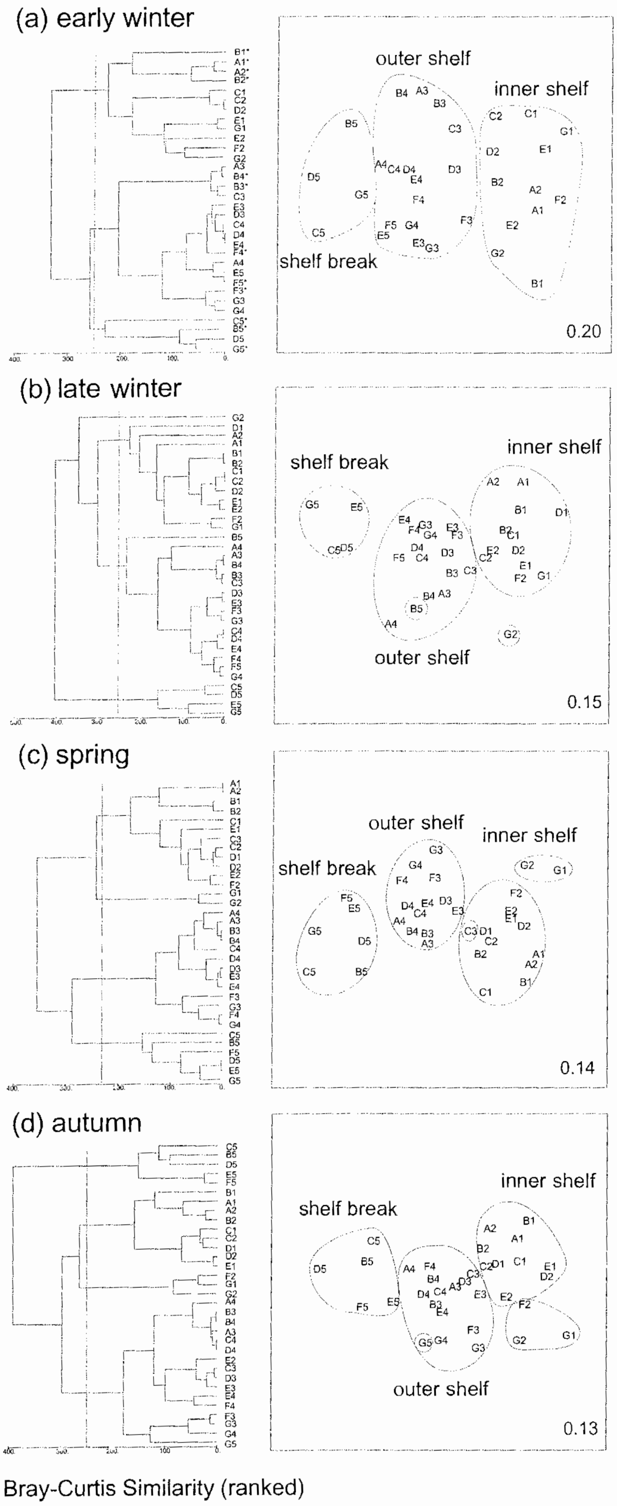


Fig. 2. Dendrograms and two-dimensional MDS plots showing similarities between trawl samples of fishes from soft-sediment substrata at five depths (1–5) on seven cross-shelf transects (A–G) on the south-eastern Australian continental shelf. Data aggregated in four seasonal groups from *(a)* early winter, *(b)* late winter, *(c)* spring, *(d)* autumn. Groupings in MDS plots based on arbitrary cut-off points in dendrograms. (Sample codes based on transect and depth as shown in Fig. 1.)

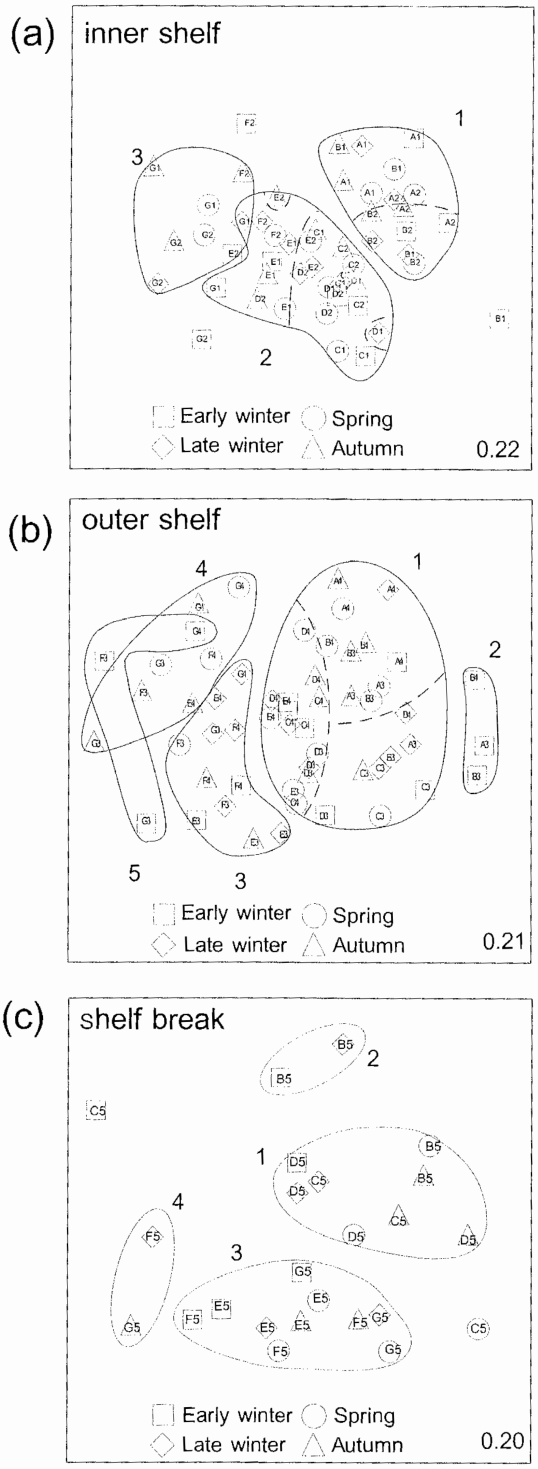


Fig. 3. Two-dimensional MDS plots showing similarities between trawl samples of fishes from soft-sediment substrata on the south-eastern Australian continental shelf. Seasonal data aggregated in three depth-related groups from *(a)* inner shelf depths 1 and 2 (25 and 40 m), *(b)* outer-shelf depths 3 and 4 (80 and 120 m), and *(c)* shelf-break depth 5 (~150–200 m) from the seven cross shelf transects (A–G) shown in Fig. 1. Groupings in MDS plots based on arbitrary cut-off points in dendrograms (not shown).

shelf and outer shelf/shelf break mesohabitats separately (Fig. 4*b* and 4*c*, respectively). These groups were clearly influenced by substratum type ('R', 'H' and 'S' from acoustics) and, at Point Hicks and the Horseshoe, their megahabitat location (Fig. 4*a*–*c*). In our orientation of the MDS-plots, substratum type similarity tended to be expressed across the horizontal axes, and megahabitat similarity on the vertical axes (Fig. 4*b*, 4*c*).

The high dissimilarity of the Point Hicks (PH) mesohabitats (PHR, PHS) to the remaining samples and to each other was the strongest feature overall (Fig. 4*a*). These samples were removed from the separate inner shelf analysis (Fig. 4*b*) because they collapsed the two-dimensional plot. Of the remaining inner-shelf samples, the Black Head (BH) and Disaster Bay (DB) megahabitats were delineated mostly by seabed type (BHH with BHR, DBR; DBH with BHS, DBS) (Fig. 4*b*). There were similar patterns among outer shelf/shelf break mesohabitats (Fig. 4*c*) where the dissimilarity of the Horseshoe (HO) megahabitat (HOS, HOH, HOR) was an obvious feature. Seabed type clearly influenced the groups formed from the remaining mesohabitats at Big Gutter (BG) and Gabo Reef (GR): BGR, GRR with GRH; BGH with BGS, GRS.

These patterns delineate seven fish communities from different substratum types within the megahabitat areas. They are coded for comparative and mapping purposes as Point Hicks soft-sediment and rock/reef substrata (PHS and PHR, respectively), inner-shelf soft-sediment and rock/reef substrata (IS and IR, respectively), outer-shelf soft-sediment and rock/reef substrata (OS and OR, respectively), and all samples from the Horseshoe (H) (and see communities 8–14 in Table 2).

Species characterizing fish communities from soft-sediment substrata

The seven communities from soft sediment substrata were species-rich, containing between 49 and 80 species (Table 3) of the total 186 species caught. Many species were widely distributed and were components of more than one community; 17 species were ubiquitous (occurring in all communities). There were 46 dominant species (making up ~70% biomass in each community and highly ranked by geometric mean abundance), 29 typifying species and 25 discriminating species (based on arbitrary cut-off values of percentage similarity: >5% and >2.3, respectively) (Table 3). Differences between communities were examined only within depth zones (inner shelf, outer shelf or shelf break). Communities were delineated mostly by the differing abundances of shared species (Table 3), many of which have strong depth-related distributions (Table 4). In general, the most typical species were also the most abundant. Restricted species were not informative: the great majority of the 53 species identified are widely distributed in temperate waters and occurred at low abundance (often single individuals).

The weak seasonal signal detected in shelf-break communities (winter *v*. spring/autumn) (Fig. 3*c*) resulted from variable catches of some abundant species and the presence/absence of many minor species. Most of the species that collectively contributed the majority (> 80%) of dissimilarity between seasons were present in both seasons (33 of 39 in SBS; 32 of 37 in SBN), whereas most remaining species were present in only one (27 of 35 in SBS; 24 of 33 in SBN). Moreover, of the eight discriminating shelf-break species (Table 3), only redfish was significantly more abundant in one or other season ($P < 0.01$, df = 10, using

Table 2. Fish communities identified by multivariate analysis of trawl samples from soft-sediment substrata (1–7) and targeted gill-net samples from different substrata (8–14) on the south-eastern Australian continental shelf

Component trawl sample codes based on transects (A–G) and depths (1–5) (see Fig. 1), and gill-net sample codes on megahabitat location (see Fig. 1) and acoustic bottom type: 'rough' (R), 'hard' (H) and 'soft' (S). Fish community codes based on depth, location and substratum type as detailed in 'Description'

Sampler	Community no.	Component samples	Community code	Description
Trawl	1	A1-2, B1-2	ISW	Inner shelf, south-west
	2	C1-2, D1-2, (E1-2)	IC	Inner shelf, central
	3	F1-2, G1-2	INE	Inner shelf, north-east
	4	A3-4, B3-4, C3-4, D3-4, (E3-4)	OSW	Outer shelf, south-west
	5	F3-4, G3-4	ONE	Outer shelf, north-east
	6	B5, C5, D5	SBS	Shelf break, southern
	7	E5, F5, G5	SBN	Shelf break, northern
Gillnet	8	PHS	PHS	Inner shelf, soft, Point Hicks
	9	PHR	PHR	Inner shelf, rough, Point Hicks
	10	BHS, DBS, DBH	IS	Inner shelf, soft/ hard, Black Head/ Disaster Bay
	11	BHR, BHH, DBR	IR	Inner shelf, hard/rough, Black Head/ Disaster Bay
	12	BGS, BGH, GRS	OS	Outer shelf, soft/hard, Big Gutter, Gabo Reef
	13	BGR, GRH, GRR	OR	Outer shelf, hard/ rough, Big Gutter, Gabo Reef
	14	HOS, HOH, HOR	H	Shelf break, soft/ hard/rough, Horseshoe

t-tests of log-transformed biomass), being present in SBS in spring/autumn but absent in winter.

Species characterizing communities from different substrata in megahabitats

Relatively few species were represented in megahabitat samples because the gill-net was more species-selective and had a lower overall catch-rate than the trawl, and because fewer samples were taken (Table 5). Communities were made up of between 11 and 46 species from the total of 87 caught (Table 5). Again, many species were widely distributed and were components of more than one community; no species was ubiquitous, but jack mackerel, piked spurdog and redfish occurred in six of the seven communities. There were 20 dominant species (making up >80% biomass and highly ranked by geometric mean abundance), 17 'typifying' species and 11 discriminating species (based on arbitrary cut-off values of percentage similarity: >6% and >5%, respectively) (Table 5). As for soft-sediment substrata , differences between communities were assessed only within depth zones (inner shelf, outer shelf or shelf break). Arbitrary cut-off values of percentage similarity were higher than for soft-sediment substrata samples because the fewer total species each contributed a greater proportion to the total similarity.

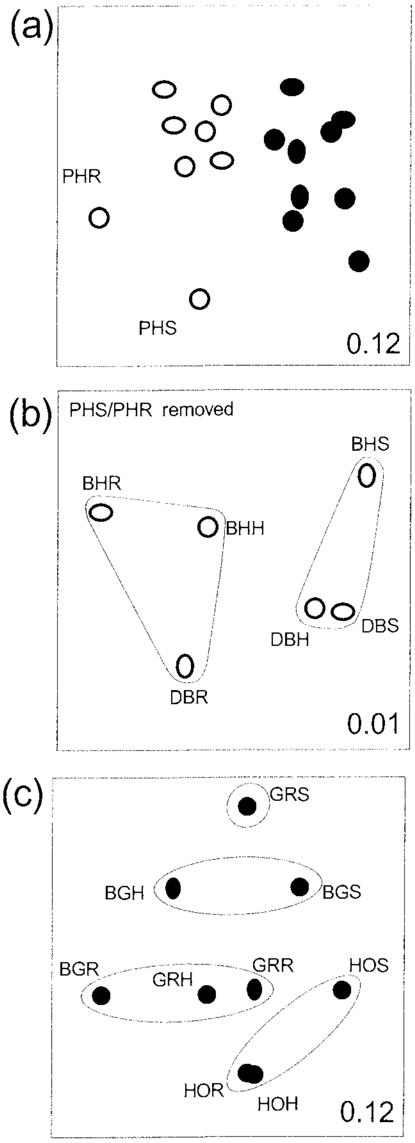


Fig. 4. Two-dimensional MDS plots showing similarities between gill-net samples of fishes from areas of different (soft-sediment and rock/reef) substrata (mesohabitats) on the south-eastern Australian continental shelf: *(a)* all samples showing (○) inner shelf and (●) outer shelf; *(b)* inner shelf samples re-analysed separately with the highly dissimilar Point Hicks samples (PHR, PHS) ommitted; *(c)* outer shelf samples re-analysed separately. Sample codes based on megahabitat location (see Fig. 1) and acoustic bottom type: 'rough' (R), 'hard' (H) and 'soft' (S). Groupings in MDS plots based on arbitrary cut-off points in dendrograms (not shown).

Several 'restricted' species from megahabitat samples were informative about community composition (Table 5), unlike soft-sediment substrata samples where 'restricted' species were of low abundance and widely distributed. Nine restricted IR species have distinct or strong reef-associations, whereas three species characteristic of the upper slope (hapuku, gemfish and deepsea flathead) were restricted to the Horseshoe.

Biophysical mapping

Community distributions were bounded in a biophysical map for the study area (the 'Twofold Shelf' meso-scale bioregion) by using distributions of seabed substrata derived from Bax and Williams (2001). The locations of samples contributing to each community and the distributions of substrata are shown in Fig. 5, and the derived map is shown in Fig. 6.

Whereas multiple gear types are needed to sample the range of substratum types, the multiple data sets they generate need to remain separate because of differences in gear selectivity. Two consequences are a spatial overlap of some of the communities defined and some inconsistencies in the placement of boundaries. Spatial overlap results because the smaller spatial scales of soft-sediment substratum communities identified by gill-net sampling (PHS, IS and OS) remain nested within the larger trawl-defined communities (IC, INE and ONE, respectively) (Fig. 6). This reflects the difference in sampling density with the two gears (Fig. 5). All community boundaries in our map necessarily approximate the transitional zones they represent. Boundaries based on bathymetric and latitudinal patterns in multispecies distributions on soft-sediment substrata are most approximate, whereas those based on hard substrata with clearly defined margins are most realistic, particularly for the many reef-associated species.

Despite combining broad-scale and targeted sampling in our survey design, some distinctive habitats were unsampled. Areas of sandstone/limestone, granite and

Table 3. Dominant, typical (T) and discriminating (D) species in communities defined by similarities of trawl samples from soft-sediment substrata on the south-eastern Australian continental shelf

Community codes follow Table 2. Species ranked by geometric mean abundance with cut-off at ~70% of total untransformed (raw) biomass (g m^{-2} × 1000); *N*, number of trawl samples; total species, number of species caught in community; typical and discriminating species based on arbitrary cut-off values of percentage similarity (>5% and >2.3, respectively) in SIMPER analysis

Community	*N*	Total species	Dominant species	Scientific name	Geo. mean biomass	% raw biomass	Cum. % biomass	T	D
ISW	16	77	Jack mackerel	*Trachurus declivis*	1063.9	39.5	39.5	*	INE; IC
			Globefish	*Diodon nicthemerus*	299.9	3.1	42.6	*	INE
			Draughtboard shark	*Cephaloscyllium laticeps*	119.0	2.9	45.5	*	INE
			Silverbelly	*Parequula melbournensis*	70.1	1.8	47.4	*	INE; IC
			Common stinkfish	*Synchiropus calauropomus*	63.2	2.2	49.6	*	INE
			Sparsely-spotted stingaree	*Urolophus paucimaculatus*	62.9	0.9	50.5	*	
			Degens leatherjacket	*Thamnaconus degeni*	61.5	3.1	53.6	*	INE; IC
			Red mullet	*Upeneichthys vlamingii*	52.3	1.1	54.7	*	
			Longnose skate	*Raja* sp. A	39.3	0.9	55.6		
			Yellowtail horse mackerel	*Trachurus novaezelandiae*	36.5	0.9	56.6		
			Banded stingaree	*Urolophus cruciatus*	36.2	0.7	57.2		
			Ruddy gurnard perch	*Neosebastes scorpaenoides*	35.3	1.0	58.2		
			Eastern school whiting	*Sillago flindersi*	34.2	7.0	65.2		INE; IC
			Sand flathead	*Platycephalus bassensis*	23.2	1.0	66.2		
			Barracouta	*Thyrsites atun*	23.2	15.1	81.3		IC
IC	23	80	Sparsely-spotted stingaree	*Urolophus paucimaculatus*	640.9	17.5	17.5	*	
			Draughtboard shark	*Cephaloscyllium laticeps*	300.8	12.3	29.8	*	INE
			Banded stingaree	*Urolophus cruciatus*	155.5	5.9	35.7	*	INE
			Globefish	*Diodon nicthemerus*	111.2	3.1	38.8	*	
			Jack mackerel	*Trachurus declivis*	60.6	20.0	58.8	*	INE
			Ruddy gurnard perch	*Neosebastes scorpaenoides*	51.2	2.3	61.1	*	INE
			Common stinkfish	*Synchiropus calauropomus*	43.0	4.4	65.5	*	INE
			Butterfly gurnard	*Lepidotrigla vanessa*	33.0	1.0	66.5	*	
			Longnose skate	*Raja* sp. A	28.1	2.4	68.9		
			Deepwater gurnard	*Lepidotrigla mulhalli*	27.4	1.4	70.3	*	
INE	12	55	Sparsely-spotted stingaree	*Urolophus paucimaculatus*	187.3	7.1	7.1	*	
			Australian angel shark	*Squatina australis*	100.8	9.1	16.2	*	ISW; IC
			Deepwater gurnard	*Lepidotrigla mulhalli*	56.6	3.4	19.7	*	
			Jack mackerel	*Trachurus declivis*	32.7	14.9	34.6	*	
			Eastern smooth boxfish	*Anoplocapros inermis*	22.8	1.2	35.8	*	
			White trevally	*Pseudocaranx dentex*	22.5	5.7	41.4		IC
			Southern eagle ray	*Myliobatis australis*	19.3	9.9	51.4		IC
			Port Jackson shark	*Heterodontus portusjacksoni*	18.4	4.4	55.8		
			Australian burrfish	*Allomycterus pilatus*	17.9	1.5	57.3	*	
			Eastern school whiting	*Sillago flindersi*	16.7	7.8	65.1		IC
			Sixspine leatherjacket	*Meuschenia freycineti*	15.2	1.9	67.0		
			Tiger flathead	*Neoplatycephalus richardsoni*	11.5	0.9	67.8	*	
			Eastern fiddler ray	*Trygonorrhina* sp. A	11.0	1.4	69.2		
			Kapala stingaree	*Urolophus* sp. A	10.3	4.9	74.2		
OSW	32	76	Cucumberfish	*Chlorophthalmus nigripinnis*	329.9	11.2	11.2	*	ONE
			Minor gurnard	*Lepidotrigla modesta*	136.5	3.2	14.4	*	ONE
			Tiger flathead	*Neoplatycephalus richardsoni*	134.7	3.5	18.0	*	
			Longnose skate	*Raja* sp. A	129.0	2.7	20.7	*	
			Velvet leatherjacket	*Parika scaber*	111.5	5.7	26.4	*	
			Draughtboard shark	*Cephaloscyllium laticeps*	86.5	5.4	31.8	*	ONE
			Piked spurdog	*Squalus megalops*	62.0	3.3	35.1	*	ONE
			Sandyback stingaree	*Urolophus bucculentus*	28.5	3.4	38.6		ONE
			Silver dory	*Cyttus australis*	27.8	1.9	40.5		
			Deepwater gurnard	*Lepidotrigla mulhalli*	25.6	2.2	42.7		
			Jack mackerel	*Trachurus declivis*	25.5	16.5	59.2		
			Australian burrfish	*Allomycterus pilatus*	23.1	1.3	60.4		

Table 3 contd over

Table 3. *contd.*

Community	*N*	Total species	Dominant species	Scientific name	Geo. mean biomass	% raw biomass	Cum % biomass	T	D
			Greenback stingaree	*Urolophus viridis*	17.5	3.1	63.5		ONE
			Barracouta	*Thyrsites atun*	15.9	10.1	73.7		ONE
ONE	16	57	Jack mackerel	*Trachurus declivis*	395.4	19.3	19.3	*	OSW
			Common snipefish	*Macroramphosus scolopax*	216.6	6.2	25.5	*	OSW
			Tiger flathead	*Neoplatycephalus richardsoni*	130.0	4.3	29.8	*	
			Velvet leatherjacket	*Parika scaber*	122.8	3.7	33.5	*	
			Redfish	*Centroberyx affinis*	39.6	35.3	68.8		OSW
SBS	12	55	Threespine cardinalfish	*Apogonops anomalus*	314.9	20.8	20.8	*	SBN
			Piked spurdog	*Squalus megalops*	91.1	4.2	25.0	*	SBN
			Cucumberfish	*Chlorophthalmus nigripinnis*	80.7	1.4	26.5	*	
			Spotted trevalla	*Seriolella punctata*	68.2	13.7	40.2	*	SBN
			Jack mackerel	*Trachurus declivis*	55.1	13.4	53.6	*	
			Speckled stargazer	*Kathetostoma canaster*	54.8	1.4	55.0	*	SBN
			Jackass morwong	*Nemadactylus macropterus*	51.7	7.7	62.7	*	SBN
			Mirror dory	*Zenopsis nebulosus*	23.0	1.0	63.7	*	
			Longnose skate	*Raja* sp. A	18.7	0.4	64.1	*	
			Tiger flathead	*Neoplatycephalus richardsoni*	17.3	0.6	64.6		
			New Zealand Dory	*Cyttus novaezelandiae*	16.9	0.7	65.3		
			Ocean perch	*Helicolenus percoides*	16.6	1.8	67.1		
			Southern whiptail	*Caelorinchus australis*	16.2	0.5	67.6		
			Barracouta	*Thyrsites atun*	10.9	1.5	69.0		
			Deepsea flathead	*Hoplichthys haswelli*	9.7	0.2	69.2		
			Pink Ling	*Genypterus blacodes*	9.6	0.3	69.6		
SBN	12	49	Redfish	*Centroberyx affinis*	676.4	26.2	26.2	*	SBS
			Cucumberfish	*Chlorophthalmus nigripinnis*	396.6	6.4	32.6	*	
			Jack mackerel	*Trachurus declivis*	291.5	29.1	61.7	*	SBS
			Ocean perch	*Helicolenus percoides*	230.7	4.3	66.0	*	SBS
			Threespine cardinalfish	*Apogonops anomalus*	57.8	15.1	81.1	*	

Table 4. Fishes making the greatest contribution to discrimination of communities by depth in trawl samples from soft-sediment substrata; biomass (g m^{-2} × 1000) unstandardized for numbers of samples
Community codes follow Table 2

Species	Scientific name	ISW	IC	INE	OSW	ONE	SBS	SBN
Jack mackerel	*Trachurus declivis*	1064	61	33	25	395	55	292
Globefish	*Diodon nicthemerus*	300	111	9	0	0	0	0
Draughtboard shark	*Cephaloscyllium laticeps*	119	301	8	87	3	5	0
Sparsely-spotted stingaree	*Urolophus paucimaculatus*	63	641	187	6	0	1	0
Eastern school whiting	*Sillago flindersi*	34	3	17	1	2	0	0
Southern eagle ray	*Myliobatis australis*	6	9	19	0	0	0	0
Velvet leatherjacket	*Meuschenia scaber*	15	15	5	112	123	0	0
Piked spurdog	*Squalus megalops*	0	3	0	62	0	91	23
Common snipefish	*Macroramphosus scolopax*	0	0	1	9	217	0	6
Cucumberfish	*Chlorophthalmus nigripinnis*	0	1	0	330	34	81	397
Mirror dory	*Zenopsis nebulosus*	0	0	0	0	0	23	17
Ocean perch	*Helicolenus percoides*	0	0	0	11	33	17	231
Threespine cardinalfish	*Apogonops anomalus*	0	0	0	1	2	315	58
Redfish	*Centroberyx affinis*	3	1	3	1	40	5	676
Spotted trevalla	*Seriolella punctata*	1	0	0	1	0	68	12

Table 5. Dominant, typical (T), discriminating (D) and restricted (R) species in communities defined by similarities of gill-net samples from different substrata on the south-eastern Australian continental shelf

Community codes follow Table 2. Dominant species ranked by geometric mean abundance with cut-off at ~80% of total untransformed (raw) biomass (kg h^{-1} per net fleet), 0 = <0.01; *N*, number of gill-net samples; total species, number of species comprising community; typical and discriminating species based on arbitrary cut-off values of percentage similarity (>6% and >5%, respectively) in SIMPER analysis; – indicates evaluation not possible.

Community	*N*	Total species	Dominant species	Scientific name	Geo. mean biomass	% raw biomass	Cum. % raw biomass	T	D	R
PHR	2	11	Draughtboard shark	*Cephaloscyllium laticeps*	6.14	55.6	55.6	–	–	
			Port Jackson shark	*Heterodontus portusjacksoni*	4.17	35.0	90.6	–	–	
PHS	2	12	Draughtboard shark	*Cephaloscyllium laticeps*	2.70	52.5	52.5			
			Piked spurdog	*Squalus megalops*	1.55	29.1	81.7		IS	
IS	6	37	Barracouta	*Thyrsites atun*	2.09	17.2	17.2	*	PHS; PHR	
			Jack mackerel	*Trachurus declivis*	1.84	28.0	45.2	*	PHS; PHR	
			Draughtboard shark	*Cephaloscyllium laticeps*	0.37	9.9	55.1	*		
			Southern sawshark	*Pristiophorus nudipinnis*	0.21	1.8	56.9	*		
			Blue mackerel	*Scomber australasicus*	0.17	4.6	61.5	*		
			Gummy shark	*Mustelus antarcticus*	0.08	8.4	69.9			
			Tiger flathead	*Neoplatycephalus richardsoni*	0.08	2.2	72.2			
			Warehou	*Seriolella brama*	0.07	15.2	87.3	*	PHS; PHR	
			Port Jackson shark	*Heterodontus portusjacksoni*	(0.02)	(1.7)		*		
			Australian bonito	*Sarda australis*	(0.00)	(0.3)				*
			Smooth hammerhead	*Sphyrna zygaena*	(0.00)	(1.2)				*
IR	6	46	Draughtboard shark	*Cephaloscyllium laticeps*	3.10	19.2	19.2	*		
			Warehou	*Seriolella brama*	2.43	22.5	41.7	*	PHS; PHR	
			Bastard trumpeter	*Latridopsis forsteri*	0.63	4.0	45.7	*		
			Blue morwong	*Nemadactylus douglasi*	0.61	3.5	49.2	*		
			Jack mackerel	*Trachurus declivis*	0.54	7.1	56.3	*	PHR	
			Port Jackson shark	*Heterodontus portusjacksoni*	0.47	10.3	66.6	*	PHS	
			Barracouta	*Thyrsites atun*	0.39	7.9	74.5	*	PHR	
			Butterfly perch	*Caesioperca lepidoptera*	0.32	1.8	76.3	*		
			Orange-spotted catshark	*Asymbolus* sp. D	0.07	0.5	76.8			
			Jackass morwong	*Nemadactylus macropterus*	0.04	1.9	78.7			
			Sergeant Baker	*Aulopus purpurissatus*	0.04	0.4	79.1			
			Piked spurdog	*Squalus megalops*	0.04	1.0	80.1			
			Banded morwong	*Cheilodactylus spectabilis*	(0.00)	(0.2)				*
			Blackbanded seaperch	*Hypoplectrodes annulata*	(0.00)	(0.0)				*
			Bluethroat wrasse	*Notolabrus tetricus*	(0.01)	(0.7)				*
			Common bullseye	*Pempheris multiradiatus*	(0.01)	(0.1)				*
			Halfbanded seaperch	*Hypoplectrodes maccullochi*	(0.00)	(0.0)				*
			Maori wrasse	*Ophthalmolepis lineolata*	(0.01)	(0.3)				*
			Snapper	*Pagrus auratus*	(0.00)	(0.0)				*
			Splendid perch	*Callanthias australis*	(0.01)	(0.1)				*
			Yellowtail kingfish	*Seriola lalandi*	(0.00)	(0.2)				*
OS	6	15	Jack mackerel	*Trachurus declivis*	0.45	69.8	69.8	*		
			Piked spurdog	*Squalus megalops*	0.22	16.2	86.0	*		
			Jackass morwong	*Nemadactylus macropterus*	(0.03)	(1.3)		*		
										*
OR	6	27	Piked spurdog	*Squalus megalops*	1.42	28.8	28.8	*		
			Jackass morwong	*Nemadactylus macropterus*	1.34	22.0	50.7	*	OS	
			Jack mackerel	*Trachurus declivis*	0.64	13.7	64.4	*		
			Barracouta	*Thyrsites atun*	0.24	9.9	74.4	*	OS	

Table 5 contd over

Table 5. *contd.*

Community	*N*	Total species	Dominant species	Scientific name	Geo. mean biomass	% raw biomass	Cum. % raw biomass	T	D	R
			Orange-spotted catshark	*Asymbolus* sp. D	0.06	2.0	76.4	*	OS; H	
			Ocean perch	*Helicolenus percoides*	0.04	0.7	77.2	*		
			Eastern orange perch	*Lepidoperca pulchella*	0.02	1.5	78.7	*	OS	
			Tiger flathead	*Neoplatycephalus richardsoni*	0.02	1.3	80.0			
			Butterfly perch	*Caesioperca lepidoptera*	(0.02)	(5.1)			OS	
			Warehou	*Seriolella brama*	(0.02)	(4.3)			OS	
H	6	24	Piked spurdog	*Squalus megalops*	1.76	15.7	15.7	*		
			Warehou	*Seriolella brama*	1.50	24.3	40.1	*	OS; OR	
			Tiger flathead	*Neoplatycephalus richardsoni*	0.88	16.4	56.5	*	OS; OR	
			Jackass morwong	*Nemadactylus macropterus*	0.79	7.2	63.7	*	OS	
			Barracouta	*Thyrsites atun*	0.48	13.3	77.0	*	OS	
			Jack mackerel	*Trachurus declivis*	0.40	9.7	86.7	*		
			Spotted warehou	*Seriolella punctata*	(0.02)	(2.8)		*	OS; OR	
			Hapuku	*Polyprion oxygeneios*	(0.01)	(1.5)				*
			Gemfish	*Rexea solandri*	(0.01)	(1.1)				*
			Deepsea flathead	*Hoplichthys haswelli*	(0.00)	(0.0)				*

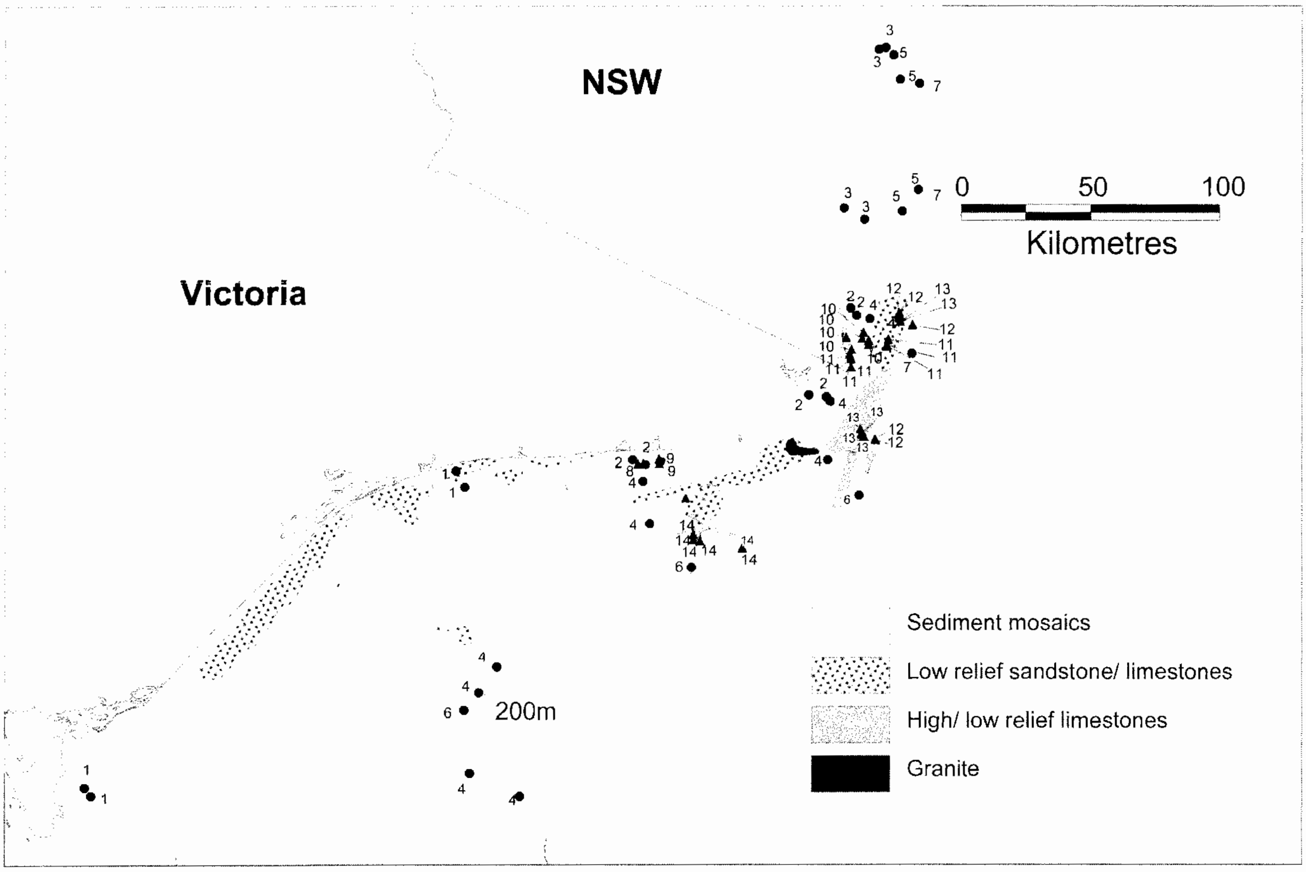


Fig. 5. Map showing locations of trawl samples from soft-sediment substrata (circles) and gill-net samples from different (soft-sediment and rock/reef) substrata (triangles) overlaid on a coarse-scale map of substrata (from Bax and Williams 2001). Samples labelled 1–14 according to fish communities in Table 2.

bryozoan-consolidated sediments supporting colonies of stalked crinoids (coded 'SL', 'G' and 'C' respectively in Fig. 6) were identified after biological sampling had been completed.

Discussion

Community structure

The demersal fish assemblage of the south-eastern Australian continental shelf can be divided into a suite of communities that, at a spatial scale of 10s to 100s of kilometres, correlates with depth, latitude and substrate type. Fish communities are generally species-rich, comprising up to 80 species. This reflects both the high overall richness of the temperate Australian ichthyofauna (Paxton *et al.* 1989; Yearsley *et al.* 1994) and the location of the study area in a faunal transition zone; the South Eastern Biotone where elements of cool temperate and warm temperate faunas overlap (IMCRA 1998). Many abundant species occur in several communities, and it was the differences in abundances of these abundant 'shared' fishes that contributed most to dissimilarity between communities. Community differentiation based on abundant fishes is more robust than one based on uncommon species that may represent sampling artefacts (Greenstreet and Hall 1996).

The strong correlation of community structure with depth is consistent with general patterns found in fish communities (see references in Connell and Lincoln-Smith 1999; Gaertner *et al.* 1999; Williams *et al.* 2001), including those from other parts of the temperate Australian shelf. Off the southern west coast (~33°S), Hyndes *et al.* (1999) found that the fish assemblage in depths of 5–15 m differed markedly from those in near-shore depths (<2 m) and further offshore (20–35 m). Off the east coast (~34°S), Gray and Otway (1994) found that assemblages in 30–60 m differed from those at 100 m depth, whereas Connell and Lincoln-Smith (1999) found a gradient in composition between three assemblages separated by 10 m intervals in the 20–70 m depth range. Our data from a broader depth range (25–~200 m) show that depth-related patterns in composition continue to the shelf break both on rock/reef and soft-sediment substrata.

Strong latitudinal (south-west/north-east) patterns in communities across the shelf agree with the classification of this region as a faunal transition zone or biotone (IMCRA

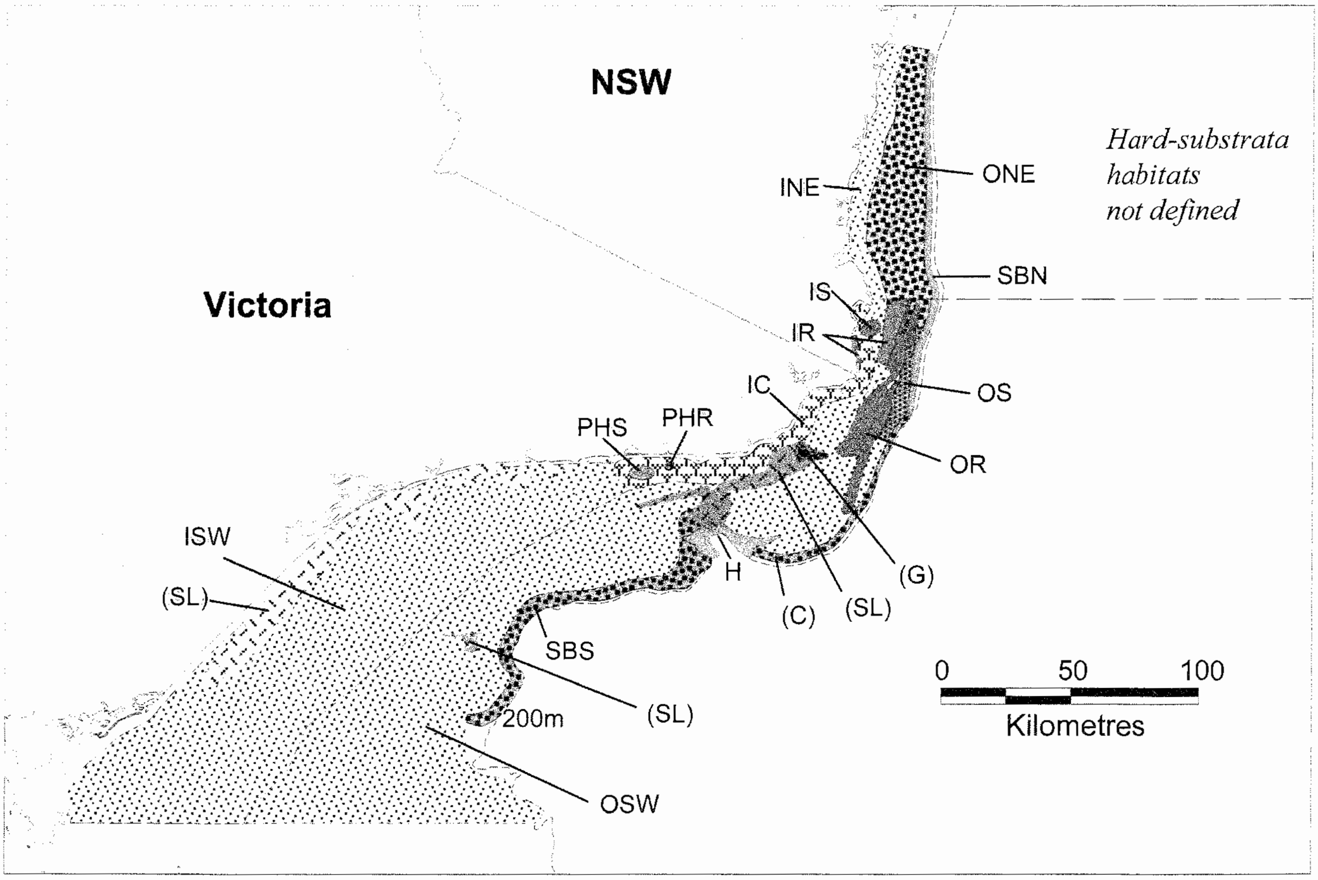


Fig. 6. Preliminary map of biophysical substructure on the south-eastern Australian continental shelf based on the conjunction of fish communities and distribution of substrata. Codes for mapped areas follow Table 2, except for those in parentheses that were not sampled for fishes: additional areas of (SL) sandstone outcrop/limestone reefs, (G) granite outcrop, (C) bryozoan-consolidated sediments supporting colonies of stalked crinoids.

1998). In addition, the location of a latitudinal boundary in the vicinity of transects D and E supports the suggestion that a major faunal disjunction occurs near Cape Howe (IMCRA 1998). Importantly, our data show that the boundary extends across the shelf; IMCRA demersal classifications were based mostly on near-shore species. The overlap of cool and warm temperate faunas on this region of the shelf coincides with an overlap of temperate and subtropical currents. Predominantly, these are eastward flows of cool Bass Strait water driven by westerly winds (Fandry 1983) that penetrate as far north and east as Eden (Newell 1961), and southward eddy field flows associated with the warm East Australian Current (EAC) (Huyer *et al.* 1988; Church and Craig 1998). Additionally, an underlying northward counter-current at the shelf break transports cool, subantarctic water from slope depths over the shelf (Cresswell 1994).

We anticipated changes in latitudinal community patterns between the seasonal trawl surveys because primary ocean currents have strongly seasonal flows: Bass Strait water in winter compared with spasmodic intrusions of mixed East Australian Current and subantarctic water in spring and summer (Huyer *et al.* 1988; Church and Craig 1998). However, community patterns related to latitude (and depth) were repeated despite marked seasonal shifts in water masses, particularly the longshore interface of Bass Strait and EAC waters over the inner shelf, during the study (Bax and Williams 2000). Where there were weak seasonal signals in community structure at the shelf break (winter *v.* spring/autumn: Fig. 3*c*), they did not clearly correspond to hydrological patterns. Both SBS and SBN communities (except sample G5) were inundated by cold slope water in spring, whereas SBN was inundated by warm water in autumn (Bax and Williams 2000). In winter, north/south patterns in community structure persisted during a period when cold slope water inundated the entire shelf break (strongly in late winter with early winter less certain owing to incomplete hydrological data).

Experienced local fishers report distinct seasonal movements of some abundant species including the economically important redfish, jackass morwong and blue warehou over the deep shelf. But importantly, fishers report that movements are also related to depth, substratum type and time of day, and may vary inter-annually. Seasonal changes in community composition are also reported on the inner shelf, and can be cyclic and involve clear movements of key species (Hyndes *et al.* 1999). It therefore seems likely that species-specific patterns of seasonal changes in community composition remained undetected by our sampling and that more frequent, targeted sampling is needed to evaluate the seasonal dynamics of fish communities over the deep shelf.

A relationship between community structure and substratum type across the temperate Australian shelf is consistent with general associations reported from small collections made over large areas and long periods of time (Gomon *et al.* 1994), and by direct observation (Kuiter 1993). Most individual species were caught both on soft-sediment and hard substrata, but many appear to have a strong degree of association with one or other (17 of 61 species). However, extrapolating substratum associations to higher taxonomic levels or faunas is not straightforward (e.g. Bellwood 1998; Robertson 1998). Definitions for the temperate Australian fauna cannot be based on taxonomic divisions at the family level because at least six of the 10 families represented by our 14 strongly reef-associated fishes contain species that are not reef-associated. Comparing diversity between substrata is also problematic owing to differences in selectivity and effectiveness between gears. The gill-net caught more species on hard (rock/reef) substrata than on soft sediments, whereas a higher number of species was caught on soft sediments overall because trawling is more effective than gill-net fishing (and in our study because more trawl samples were taken).

Ecological associations with habitats

Habitat may be defined simply 'as the place where an organism lives' (Hudson *et al.* 1992), or for fishes, as 'the structural component of the environment that attracts organisms and serves as a centre of biological activity' (Peters and Cross 1991; following Ryder and Kerr 1989). An important structural component of habitat for fishes is substratum complexity: high rugosity and/or vertical relief provides food and shelter from predators at spatial scales of reefs (Jones 1988; Hixon and Beets 1993; Ohman and Rajasuriya 1998) and microtopography (Lough *et al.* 1989; Auster *et al.* 1995, 1997). We suggest that another important structural component of fish habitat on the south-eastern Australian shelf, based on patterns of functional morphology in fishes, is the prevailing hydrodynamic climate: its local-scale interactions with substratum composition and topography, and larger-scale influence on food supply.

Fishes of inner-shelf soft-sediment communities (ISW, IC, INE, PHS, IS) inhabit plains of predominantly unconsolidated quartz and carbonate sands (Davies 1979; Jones and Davies 1983). These, together with other components including mollusc beds and accumulations of shell debris (Bax and Williams 2001), form vast habitats with relatively low substratum complexity. Relatively small, interspersed areas of low-relief (<2 m) sandstones and limestone reefs and occasional outcrops of high-relief (<20 m) granite (Bax and Williams 2001) are habitats for distinct hard-substratum communities; the PHR community on granite outcrops off Point Hicks and IR on the limestone reefs that form the inner and outer margins of Disaster Bay.

Inner-shelf seabed habitats are hydrodynamically energetic, being influenced by high-energy wind-waves

(Wright 1995) and wind-driven currents (Fandry 1983). On the southern coast, where average waves are 1–3 m height (Morrow and Jones 1988) and strong currents (>50 cm s^{-1}) are driven by westerly winds and gales (Fandry 1983), the seabed is affected to a depth of at least 60 m. The change from unrippled, muddy sands off Wilsons Promontory to strongly rippled (~10–30 cm wavelength and amplitude), well sorted coarse sands with accumulations of shell debris east of Point Hicks (Bax and Williams 2001) demonstrates the eastwards increase in flow velocity and tidal currents predicted by Fandry (1983).

Inner-shelf communities occupying current-swept habitats with low structural complexity (ISW, IC, INE, PHS, IS) are dominated by morphotypes with flow-related morphology (Bax *et al.* 1999*b*), well adapted for effective locomotion and station-holding (Arnold and Weihs 1978; Webb 1989). Stingarees and angel shark combine undulatory swimming with extreme dorso-ventral flattening to provide a 'low-drag, high-lift' form (Webb 1989). Sustained (caudal) swimming capability with fusiform morphology enables jack mackerel, spurdog, barracouta and warehou to use the overlying water column (Bax *et al.* 1999*b*), and substratum ripples may provide energetically efficient flow-refuges (Gerstner 1998) for small bodied and elongate burst-swimmers such as stinkfish and whiting. Dominant fishes from the structurally complex habitat provided by limestone reefs adorned with 'gardens' of attached sponge, seawhip and bryozoan communities (Bax and Williams 2001) include laterally compressed manoeuverers with well developed pectoral fins for oscillatory swimming (Bax *et al.* 1999*b*): bastard trumpeter, blue morwong and butterfly perch.

The interaction of prevailing currents with larger topographic features influences the production sources for demersal shelf fishes; nutrients and key prey are greatest over the deep shelf where subantarctic water is uplifted from the slope (Bax and Williams 2000). High secondary production is indicated by the abundance of several shelf fishes—small forage fishes and large predators—that prey on pelagic plankton and micronekton, many species of which appear to be oceanic in origin (Bulman *et al.* 2001). Flows of food-rich water can be modified at local scales by topographic features to produce productive fishing grounds such as the canyon head at the 'Horseshoe' (Bax and Williams 2001).

Collectively, these patterns suggest that strength of water currents and levels of current-borne food are structural attributes of habitats that help shape shelf fish communities. We suggest that the role played by substratum complexity in providing refuge from flow is worthy of further attention in the context of examining fish habitat on the continental shelf. Water currents can be modelled as a quantitative attribute of habitat for mapping purposes and can be rapidly measured during surveys with research vessels.

Management implications

Scale is an important component of managing natural resources. Understanding the scales of biodiversity, especially those related to habitat, is seen as essential for identifying an ecologically or biogeographically representative system of protected areas in Australia (ANZECC TFMPA 1999*a*). A hierarchy of scaled ecological units has been proposed for Australia's National Representative System of Marine Protected Areas (NRSMPA). These scaled ecological units are: bioregion, ecosystem, habitat, community/population and species/individual (ANZECC TFMPA 1999*b*). This set does not represent a coherent, or fully nested, hierarchy and it will take some time to establish its use in practice. Only bioregions have been defined to date. Twofold Shelf, the 32 198 km^2 bioregion that contains the area of this study, is one of 60 bioregions identified in the NRSMPA. Less than 1 km^2 of the Twofold Shelf bioregion is set aside as a marine protected area (MPA).

The NRSMPA is based on the concept of holistic, integrated ecosystem management. Unfortunately, ecosystem management is a very loosely defined construct, which means different things to different individuals based on their culture, experience and interests. Embraced in the 1990s by conservationists, who heard 'ecosystem', and by industry representatives, who heard 'management', the term may be falling out of favour owing to lack of common agreement on what the term really means (Yaffee 1999). We do not attempt to further define ecosystem management here, but instead use Odum's (1953) original definition of an ecosystem as 'any entity or natural unit that includes living and non-living parts interacting to produce a stable system in which the exchange of materials between the living and non-living parts follows circular paths' as the basis for our discussion. In doing so we note that ecosystem-based management requires integration of environmental and developmental planning within a management unit. The critical factor is defining the management unit (Langton *et al.* 1995), which is what we attempt below.

The physical process dominating the exchange of materials between the living and non-living components in the Twofold Shelf bioregion is ocean circulation. There is, for example, little input of nutrients from terrestrial or estuarine sources to the continental shelf (Bax *et al.* 2001). But at the shelf break, the East Australia Current drives deep upwelling of nutrient-rich slope water that is associated with plankton blooms. The continental shelf from an undefined depth (but less than 25 m) to the edge of the shelf at 170–250 m appears to represent a natural unit and could be considered one (relatively open) ecosystem within the Twofold Shelf bioregion.

Within this ecosystem, the four major correlates of spatial variation in fish community structure are latitude, depth, seabed type and hydrography; spatial organization in benthic invertebrate communities appears to be quite similar (Bax and Williams 2000). Spatial variation in communities associated with depth is crossed with that associated with latitude; inner shelf, outer shelf and shelf break communities were described in both the eastern and western areas of the study area. Spatial variation associated with hydrography and seabed type is nested within latitude and depth. Regardless of the definition used for habitat in the hierarchy of scaled ecological units developed for the NRMPA—seabed type, hydrographic area, or depth—habitat and community are interwoven. A more rigorous definition may be required if the scaled ecological units are to have application in describing ecological units in a hierarchical sense.

The primary goal of the NRSMPA is to commit jurisdictions to establishing and managing a comprehensive, adequate and representative system of MPAs (ANZECC TFMPA 1999*a*). Comprehensive implies recognizing the full range of ecosystems; adequate implies developing MPAs of sufficient size to ensure the ecological viability and integrity of populations, species and communities; and representative implies that selected areas should reasonably reflect the biotic diversity of the marine ecosystems that they are part of. Based on the results of this study, this would imply that distinct management units can be defined for three different depths, and two different latitudinal groups. Within these management units, special consideration should be given to particular hydrographic regimes and habitats associated with distinctive communities. In addition, it is also clear that this ecosystem is fairly open. Whereas a system of MPAs could help sustain vulnerable habitats, a different level of management will continue to be required to sustain the more mobile fish, bird and mammal species. Species/individual is the lowest level ecological unit in the NRMPA hierarchy.

Developing a representative system of MPAs is just one of the potential uses of ecologically determined management units. As these management units are based on the distribution of fish communities, they also have relevance to the interpretation of catch per unit effort data for single species fisheries management and managing discarding of unwanted fish for wider environmental (or societal) objectives. Because the distribution of fish communities is correlated with many of the same biophysical properties that correlate with invertebrate communities (Bax and Williams 2000), these management units also have relevance to surveys and interpretation of marine biodiversity, although additional axes of distribution may need to be included for such uses.

Considerable resources were spent in mapping the ecosystem in this area, including using a research vessel and chartered commercial vessels for several weeks at sea, and the area is just part of one ecosystem in one of 60 bioregions. It is doubtful whether a similar level of resources would be available for mapping the majority of Australia's bioregions. Surrogates will be necessary to achieve this in many instances. Maps of seabed type developed in cooperation with commercial fishers provide the basis for one method of inferring community composition (Bax and Williams 2001). In our map of communities (Fig. 6) we have identified areas of sandstone/limestone reefs, granite outcrops and bryozoan colonies that we did not survey, yet could start to predict the fish communities that occur there. But seabed type is just one of the variables affecting fish and invertebrate community composition. It is necessary to interpret maps of seabed type in the context of the broader depth and latitudinal community structure in which they occur as well as how they may be modified by local hydrography.

The seascape, like the terrestrial landscape, has evolved through long processes of accretion, consolidation, biogenic activity and weathering. Fishes live in the interface between this intricate landscape and the overlying water column that has its own complex structure, controlling food availability, modifying substrate topography and determining the energy required to survive in this highly energetic environment. Fish have evolved adaptations to their environment and this has resulted in the diversity of forms that occur today in the different communities on the south-eastern Australian shelf. Managing these communities will require attention to the factors that enable their existence. In this paper, we have provided a first analysis of these factors.

Acknowledgments

We gratefully acknowledge the assistance of several colleagues at CSIRO Marine Research for assistance with various areas of a larger project that provided material for this paper, particularly Dr Alan Butler and Ms Franzis Althaus for comments on an earlier draft, and Bruce Barker who prepared the figures. In addition, we thank the officers and crew of the RV *Southern Surveyor* who ran the vessel during the field surveys. We are indebted to several commercial fishers and operators in the fishing industry from Eden in New South Wales and Lakes Entrance in Victoria for help with field sampling, especially Horst Fischer, Nick Albers and Kevin Haslam and their crews during charters of their vessels. Many other commercial operators generously provided information that helped us to plan our field sampling and interpret results. This work was part of a larger study funded in part by the Fisheries Research and Development Corporation, project no. 94/040.

References

ANZECC TFMPA (1999*a*). Strategic plan of action for the national representative system of marine protected areas. (Environment Australia: Canberra.)

ANZECC TFMPA (1999*b*). Understanding and applying the principles of comprehensiveness, adequacy and representativeness for the NRSMPA, Version 3.1. Report generated by the Action Team for the ANZECC Task Force on Marine Protected Areas. (Marine Group, Environment Australia: Canberra.)

Arnold, G. P., and Weihs, D. (1978). The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa*). *Journal of Experimental Biology* **75**, 147–69.

Auster, P. J. (1988). A review of the present state of understanding of marine fish communities. *Journal of Northwest Atlantic Fisheries Science* **8**, 67–75.

Auster, P. J., and Malatesta, R. J. (1995). Assessing the role of non-extractive reserves for enhancing harvested populations in temperate and boreal marine systems. In 'Marine Protected Areas and Sustainable Fisheries'. (Eds N. L. Shackell and J. H. M. Wilson.) pp. 82–9. (Science and Management of Protected Areas Association: Wolfville, Novia Scotia, Canada.)

Auster, P. J., Malatesta, R. J., and LaRosa, S. C. (1995). Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. *Marine Ecology Progress Series* **127**, 77–85.

Auster, P. J., Malatesta, R. J., and Donaldson, C. L. S. (1997). Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. *Environmental Biology of Fishes* **50**, 195–200.

Barker, B. A. J., Helmond, I., Bax, N. J., Williams, A., Davenport, S., and Wadley, V. A. (1999). A vessel-towed camera platform for surveying seafloor habitats of the continental shelf. *Continental Shelf Research* **19**, 1161–70.

Bax, N. J., and Williams, A. (Eds) (2000). Habitat and fisheries productivity in the South East Fishery. Final report to FRDC Project 94/040. (CSIRO Marine Research: Hobart, Australia.)

Bax, N. J., and Williams, A. (2001). Seabed habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring. *Marine and Freshwater Research* **52**, 491–512.

Bax, N., Kloser, R. J., Williams, A., Gowlett-Holmes, K., and Ryan, T. (1999*a*). Seafloor habitat definition for spatial management in fisheries: a case study on the continental shelf of southeast Australia using acoustics and biotic assemblages. *Oceanologica Acta* **22**, 707–19.

Bax, N. J., Williams, A., and Althaus, F. (1999*b*). Development of a rapid-assessment technique to determine biological interactions of fishes, and their environment and their role in the ecosystem. Final Report to Fisheries Research and Development Corporation, Project No: 96/275. (CSIRO Marine Research: Hobart, Australia.) 149 pp.

Bax, N. J., Burford, M., Clementson, L., and Davenport, S. (2001). Phytoplankton blooms and productivity on the south-east Australian continental shelf. *Marine and Freshwater Research* **52**, 451–62.

Bellwood, D. R. (1998). What are reef fishes? Comment on the report by D. R. Robertson: do coral-reef fishes faunas have a distinctive taxonomic structure? (Coral Reefs 17, 179–86). *Coral Reefs* **17**, 187–9.

Bulman, C., Althaus, F., He, X., Bax, N. J., and Williams, A. (2001). Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine and Freshwater Research* **52**, 537–48.

Carr, M. R. (1996). 'PRIMER User Manual; Plymouth Routines in Multivariate Ecological Research.' (Plymouth Marine Laboratory: Plymouth, England.)

Caton A., McLoughlin K., and Staples D. (Eds) (1997). Fishery status reports 1997: resources assessments of Australian Commonwealth fisheries. (Bureau of Resource Sciences: Canberra, Australia.) 139 pp.

Church, J. A., and Craig, J. D. (1998). Australia's shelf seas: diversity and complexity. In 'The Sea, Vol. 11'. (Eds A. R. Robinson and K. H. Brink.) pp. 933–64. (John Wiley: New York.)

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal Ecology* **18**, 117–43.

Connell, S. D., and Lincoln-Smith, M. P. (1999). Depth and the structure of assemblages of demersal fish: experimental trawling along a temperate coast. *Estuarine, Coastal and Shelf Science* **48**, 483–95.

Cresswell, G. (1994). Nutrient enrichment of the Sydney continental shelf. *Australian Journal of Marine and Freshwater Research* **45**, 677–91.

Davies, P. J. (1979). Marine geology of the continental shelf off southeast Australia. Department of National Resources, Bureau of Mineral Resources, Geology and Geophysics. Australian Government Publishing Service, Canberra, Bulletin No. 195.

Environment Australia (1998). 'Australia's Oceans Policy.' (Environment Australia: Canberra.) 48 pp.

Fandry, C. B. (1983). Model for the three-dimensional structure of wind-driven and tidal circulation in Bass Strait. *Australian Journal of Marine and Freshwater Research* **34**, 121–41.

Gaertner, J. C., Mazouni, N., Sabatier, R., and Millet, B. (1999). Spatial structure and habitat associations of demersal assemblages in the Gulf of Lions: a multicompartmental approach. *Marine Biology* **135**, 199–208.

Garcia-Charton, J. A., and Perez-Ruzafa, A. (1999). Ecological heterogeneity and the evaluation of the effects of marine reserves. *Fisheries Research* **42**, 1–20.

Gerstner, C. L. (1998). Use of substratum ripples for flow refuging by Atlantic cod, *Gadus morhua*. *Environmental Biology of Fishes* **51**, 455–60.

Gomon, M. F., Glover, J. C. M., and Kuiter, R. H. (1994). 'The Fishes of Australia's South Coast.' (State Printer: Adelaide.)

Gray, C. A., and Otway, N. M. (1994). Spatial and temporal difference in assemblages of demersal fishes on the inner continental shelf off Sydney, south-eastern Australia. *Australian Journal Marine Freshwater Research* **45**, 665–76.

Greene, H. G., Yoklavich, M. M., Starr, R. M., O'Connell, V. M., Wakefield, W. W., Sullivan D. E., McRea, J. E. Jnr, and Cailliet G. M. (1999). A classification scheme for deep seafloor habitats. *Oceanologica Acta* **22**, 663–78.

Greenstreet, S. P. R., and Hall, S. J. (1996). Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology* **65**, 577–98.

Hixon, M. A., and Beets, J. P. (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* **63**, 77–101.

Holling, C. S. (1992). Cross-scale morphology, geometry and dynamics of ecosystems. *Ecological Monographs* **62**, 447–502.

Hudson, P. L., Griffiths, R. W., and Wheaton, T. J. (1992). Review of habitat classification schemes appropriate to streams, rivers, and connecting channels in the Great Lakes drainage basin. In 'The Development of an Aquatic Habitat Classification System for Lakes'. (Eds W. D. N. Busch and P. G. Sly.) pp. 73–107. (CRC Press: Ann Arbor, MI.)

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187–211.

Huyer, A., Smith, R. L., Stabeno, P. J., Church, J. A., and White, N. J. (1988). Currents off south-eastern Australia: results from the Australian Coastal Experiment. *Australian Journal of Marine and Freshwater Research.* **39**, 245–88.

Hyndes, G. A., Platell, M. E., Potter, I. C., and Lenanton, R. C. J. (1999). Does the composition of the demersal fish assemblages in temperate coastal waters change with depth and undergo consistent seasonal changes? *Marine Biology* **134**, 335–52.

IMCRA (1998). Interim Marine and Coastal Regionalisation for Australia: an ecosystem-based classification for marine and coastal environments. (Commonwealth of Australia.) 104 pp.

Jones, G. P. (1988). Ecology of rocky reef fish of north-eastern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* **22**, 445–62.

Jones, H. A., and Davies, P. J. (1983). Superficial sediments of the Tasmanian continental shelf and part of Bass Strait. Department of Resources and Energy, Bureau of Mineral Resources, Geology and Geophysics. Australian Government Publishing Service, Canberra, Bulletin No. 218.

Kerr, S. R., and Ryder, R. A. (1989). Current approaches to multispecies analyses of marine fisheries. *Canadian Journal Fisheries and Aquatic Science* **4**, 528–34.

Kloser, R. J., Bax, N. J., Ryan, T., Williams, A., and Barker, B. A. (2001). Remote sensing of seabed types in the Australian South East Fishery; development and application of normal incident acoustic techniques and associated 'ground truthing'. *Marine and Freshwater Research* **52**, 475–89.

Kuiter, R. H. (1993). 'Coastal Fishes of South-eastern Australia.' (Crawford House Press: Bathurst, Australia.) 437 pp.

Langton, R. W., Auster, P. J., and Schneider, D. C. (1995). A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. *Reviews in Fisheries Science* **3**, 201–29.

Last, P. R. L., and Stevens, J. D. (1994) 'Sharks and Rays of Australia.' (CSIRO Division of Fisheries: Australia.)

Legendre, L., and Legendre, P. (1988). 'Numerical Ecology.' (Elsevier: New York.)

Lough, R. G., Valentine, P. C., Potter, D. C., Auditore, P. J., Bolz, G. R., Neilson, J. D., and Perry, R. I. (1989). Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Marine Ecology Progress Series* **56**, 1–12.

Montevecchi, W. A., and Myers, R. A. (1995). Prey harvest of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. *Marine Ecology Progress Series* **117**, 1–9.

Morrow, R. A., and Jones, I. S. F. (1988). Sea floor drag coefficients – eastern Bass Strait. University of Sydney, Ocean Sciences Institute, Report No. **29**. 7 pp.

Moulton, P. L., and Wankowski, J. W. J. (1985). Demersal fish survey methods for eastern Bass Strait 1982–1984. Department of Conservation Forests and Lands, Victoria, Marine Science Laboratory Technical Report No. 41, 28 pp.

Newell, B. S. (1961). Hydrology of south-east Australian waters: Bass Strait and New South Wales tuna fishing area. CSIRO Division of Fisheries and Oceanography Technical Paper No. 10.

Odum, E. (1953). 'Fundamentals of Ecology.' (WB Saunders: Philadelphia.)

Ohman, M. C., and Rajasuriya, A. (1998). Relationships between habitat structure and fish communities on coral and sandstone reefs. *Environmental Biology of Fishes* **53**, 19–31.

Paxton, J. R., Hoese, D. F., Allen, G. R., and Hanley, J. E. (1989). Zoological catalogue of Australia, Vol. 7, PISCES—Petromyzontidae to Carangidae. (Australian Government Publishing Service: Canberra.)

Peters, D. S., and Cross, F. A. (1991). What is coastal fish habitat? In 'Stemming the Tide of Coastal Fish Habitat Loss'. (Ed. R. H. Stroud.) pp. 17–22. (National Coalition For Marine Conservation: Savannah, GA.)

Robertson, D. R. (1998). Do coral-reef fishes faunas have a distinctive taxonomic structure? *Coral Reefs* **17**, 179–86.

Rose, G. A., and Leggett, W. C. (1990). The importance of scale to predator–prey spatial correlations: an example of Atlantic fishes. *Ecology* **71**, 33–43.

Ryder, R. A., and Kerr, S. R. (1989). Environmental priorities: placing habitat in a hierarchical perspective. *Canadian Special Publications in Fisheries and Aquatic Sciences* **105**, 2–12.

Tilzey, R. D. J. (Ed.) (1994). 'The South East Fishery.' (Bureau of Resource Sciences: Canberra.)

Tilzey, R. D. J., and Rowling, K. R. (2001). History of Australia's South East Fishery: a scientist's perspective. *Marine and Freshwater Research* **52**, 361–75.

Walters, C., and Bonfil, R. (1999). Multispecies spatial assessment models for the British Columbia groundfish trawl fishery. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 601–28.

Webb, P. (1989). Station-holding by three species of benthic fishes. *Journal of Experimental Biology* **145**, 303–20.

Williams, A., Koslow, J. A., and Last, P. R. L. (2001). Diversity, density and community structure of the demersal fish fauna of the continental slope off western Australia (20–35°S). *Marine Ecology Progress Series* **212**, 247–63.

With, K. A., and Crist, T. O. (1995). Critical thresholds in species' responses to landscape structure. *Ecology* **76**, 2446–59.

Wright, L. D. (1995). 'Morphodynamics of Inner Continental Shelves.' (CRC Press: Boca Raton, FL.)

Yaffee, S. L. (1999). Three faces of ecosystem management. Conservation Biology **13**, 713–25.

Yearsley G. K., Last, P. R. L., and Morris, G. B. (1994). The modified and upgraded species-coding system for Australian fisheries databases. Final Report to the Fisheries Research and Development Trust Fund, Canberra, 90/105.

Manuscript received 10 February 2000; revised and accepted 28 August 2000

Appendix 1. Description of the design and construction of fishing gears used in multi-gear survey of seabed types on the south-eastern Australian continental shelf

The trawl was a commercial demersal design made by McKenna net-makers of Hobart, Tasmania, for the multi-species shelf fishery off south-eastern Australia. It is a two-panel design with a total length of ~54 m, a headline of 37.6 m buoyed by 56 × 200 mm diameter floats, and a footrope of 41.3 m with ~150 mm diameter punched-disc rubber rollers. Its mesh sizes decreased from ~220 mm (9″) in the wings, square and belly to 40 mm (~2″) in the cod-end liner. In operation, the net had a wingspread of ~20 m and headline height of ~3 m (as measured by acoustic sensors) and was fished from twin warps behind Polyvalent trawl doors.

Our gill-net and traps design reflected the need to sample a wide range of species of varying sizes and vulnerability on current-swept substrates that included hard reef. The net consisted of two identical fleets of six monofilament-mesh panels of different mesh size (50, 76, 100, 125, 150, 175 mm). Their line diameters were 0.62, 0.62, 0.81, 0.9, 0.9 and1.05, respectively, and each had a hanging ratio of 0.5 and a hanging coefficient 0.87. Each of the 12 panels was 90 m long and 2.8 m deep, and separated by 40 m bridles. Net fleets were separated by 100 m bridles giving the net a total length of ~1.6 km. The ground line was heavily weighted with 38 kg lead per panel and the float line buoyed with 11.4 kg floats per panel; 20 kg grapples were used to anchor the centre and each end of the net.

Commercial style traps were based on a rectangular hardwood frame (1.8 × 1.5 × 1.2 m) covered with 40 mm narrow-gauge wire mesh with a single, inward facing wire mesh entrance cone of 550 mm diameter reducing to 300 mm, with an open slot of 300 × 50 mm. Each trap was baited with a fast-release 500 mL bait block of minced pilchard, tuna, jack mackerel and abalone, and a whole striped tuna. The bait, contained in a slotted basket, and the tuna impaled on a skewer, were positioned in the centre of the trap (about 600 mm behind the front panel). Each trap base was weighted with ~15 kg wire rope and anchored with a 20 kg grapple from a polypropelene bridle. The traps were conditioned (soaked) prior to use and maintained by re-tensioning the wire walls as necessary to prevent strumming in high currents. Typically, traps were deployed in sets of five with a spacing of ~200–300 m to give a similar spatial coverage to the gill-net.

Appendix 2. List of trawl stations from seasonal surveys of soft-sediment substrata on the south-eastern Australian continental shelf

Codes for transects and depth stratum follow Fig. 1

Survey	Station	Transect	Depth	Depth (m)	Start position		Survey	Station	Transect	Depth	Depth (m)	Start position	
		code	stratum	(start)	Latitude	Longitude			code	stratum	(start)	Latitude	Longitude
Early winter	85	A	1	24	–38.9838	146.5460	Autumn	14	A	1	21	–38.9817	146.5300
	87	A	2	41	–39.0133	146.5780		21	A	2	41	–38.9800	146.6083
	79	A	3	72	–38.9317	148.3220		31	A	3	87	–38.9567	148.3517
	81	A	4	123	–38.9767	148.4880		35	A	4	125	–38.9867	148.4983
	104	B	1	30	–37.8650	148.8660		22	B	1	27	–37.8600	148.2113
	102	B	2	42	–37.9250	148.2070		29	B	2	40	–37.9550	148.2317
	72	B	3	84	–38.7383	148.2970		13	B	3	84	–38.6917	148.3017
	74	B	4	106	–38.6400	148.3270		10	B	4	115	–38.6500	148.3317
	76	B	5	210	–38.5550	148.4280		7	B	5	190	–38.5700	148.3867
	106	C	1	28	–37.8083	149.0650		60	C	1	24	–37.8083	149.0300
	108	C	2	46	–37.8250	149.0850		55	C	2	42	–37.8300	149.0950
	110	C	3	72	–37.8733	149.1130		51	C	3	77	–37.9050	149.0650
	112	C	4	114	–38.0150	149.2150		48	C	4	113	–38.0433	149.1450
	114	C	5	210	–38.1945	149.2740		43	C	5	206	–38.2017	149.2650
	217	D	2	38	–37.5850	149.8430		84	D	1	26	–37.5833	149.8033
	215	D	3	73	–37.6467	149.8330		82	D	2	35	–37.5783	149.8717
	213	D	4	130	–37.8067	149.8980		75	D	3	89	–37.6067	149.9183
	211	D	5	220	–37.9483	150.0350		72	D	4	129	–37.8100	149.9017
	140	E	1	22	–37.2767	149.9700		67	D	5	200	–37.9483	150.0317
	130	E	2	40	–37.2950	150.0200		96	E	1	26	–37.2683	150.0033
	129	E	3	80	–37.3367	150.0580		91	E	2	45	–37.2967	150.0300
	141	E	4	115	–37.2983	150.2200		88	E	3	82	–37.2967	150.0783
	124	E	5	160	–37.4083	150.2920		107	E	4	112	–37.3117	150.2033
	160	F	2	37	–36.9217	149.9570		102	E	5	169	–37.3917	150.2983
	150	F	3	68	–36.9483	150.0420		113	F	2	42	–36.9043	149.9672
	153	F	4	115	–36.9417	150.1970		146	F	3	71	–36.9667	150.0517
	142	F	5	143	–36.9100	150.2920		156	F	4	111	–36.9567	150.2100
	259	G	1	27	–36.3517	150.1230		149	F	5	223	–36.8583	150.3083
	257	G	2	40	–36.3667	150.1450		131	G	1	26	–36.3467	150.1317
	255	G	3	77	–36.3633	150.1920		123	G	2	45	–36.3700	150.1517
	253	G	4	118	–36.4067	150.2480		128	G	3	78	–36.3867	150.1800
	251	G	5	229	–36.4070	150.3160		119	G	4	119	–36.4700	150.2367
								114	G	5	160	–36.4933	150.2900
Late winter	26	A	1	31	–38.9700	146.5700	Spring	14	A	1	26	–38.9633	146.5750
	30	A	2	43	–39.0017	146.5970		10	A	2	41	–38.9850	146.6150
	58	A	3	78	–38.9317	148.3200		239	A	3	80	–38.9150	148.3000
	56	A	4	123	–38.9933	148.5200		20	A	4	126	–38.9967	148.5234
	36	B	1	28	–37.8583	148.2200		39	B	1	26	–37.8517	148.2367
	40	B	2	41	–37.9233	148.2480		34	B	2	42	–37.8983	148.2833
	45	B	3	86	–38.7067	148.2800		22	B	3	82	–38.6983	148.2717
	47	B	4	104	–38.6517	148.3300		24	B	4	113	–38.6450	148.3333
	51	B	5	200	–38.5467	148.4140		33	B	5	219	–38.5433	148.4167
Survey	Station	Transect	Depth	Depth (m)	Start position		Survey	Station	Transect	Depth	Depth (m)	Start position	
		code	stratum	(start)	Latitude	Longitude			code	stratum	(start)	Latitude	Longitude

table contd over

Appendix 2. *contd*

72	C	1	25	–37.8100	149.0180	58	C	1	24	–37.8083	149.0383
70	C	2	43	–37.8250	149.0700	69	C	2	40	–37.8267	149.0883
66	C	3	74	–37.8900	149.0650	45	C	3	70	–37.8883	149.0717
78	C	4	118	–38.0300	149.1220	47	C	4	114	–38.0367	149.1067
82	C	5	220	–38.1960	149.2770	49	C	5	210	–38.1983	149.2617
94	D	1	24	–37.5850	149.7200	226	D	1	24	–37.5833	149.8067
92	D	2	36	–37.5883	149.8500	86	D	2	45	–37.5833	149.8950
88	D	3	90	–37.6117	149.9170	84	D	3	84	–37.5967	149.9133
100	D	4	129	–37.8150	149.8880	72	D	4	129	–37.8017	149.9017
104	D	5	220	–37.9242	150.0370	71	D	5	217	–37.9367	150.0317
126	E	1	26	–37.2850	149.9900	96	E	1	25	–37.2700	149.9967
124	E	2	44	–37.3050	150.0220	105	E	2	37	–37.2783	150.0317
115	E	3	78	–37.2783	150.0770	94	E	3	85	–37.3150	150.0800
113	E	4	115	–37.3150	150.1920	129	E	4	118	–37.3300	150.2133
111	E	5	161	–37.4317	150.2730	127	E	5	155	–37.4600	150.2583
133	F	2	41	–36.9117	149.9630	140	F	2	43	–36.9217	149.9633
135	F	3	68	–36.9567	150.0430	144	F	3	72	–36.9483	150.0483
138	F	4	120	–36.9600	150.2150	150	F	4	119	–36.9333	150.2217
145	F	5	149	–36.8750	150.3020	152	F	5	140	–36.8567	150.2983
166	G	1	25	–36.3527	150.1220	106	G	1	28	–36.3533	150.1283
164	G	2	41	–36.3600	150.1430	108	G	2	39	–36.3650	150.1450
160	G	3	81	–36.4000	150.1750	115	G	3	78	–36.3950	150.1800
154	G	4	123	–36.4617	150.2180	119	G	4	118	–36.4650	150.2167
152	G	5	247	–36.5067	150.3080	117	G	5	220	–36.4750	150.2133

Appendix 3. List of gillnet stations from surveys of sites (macrohabitats) in areas of different substrata (mesohabitats) on the south-eastern Australian continental shelf

Substratum type based on acoustically derived indices (Bax *et al.* 1999). Codes for mesohabitats follow Fig. 1

Survey	Megahabitat	Code	Mesohabitat substratum type	Mesohabitat code	Depth (m)	Net fleet samples	
						Day	Night
1	Point Hicks	PH	Soft	PHS	41	2	2
			Rough	PHR	28	2	2
	Black Head	BH	Soft	BHS	45	2	2
			Hard	BHH	40	2	2
			Rough	BHR	42	2	2
	Disaster Bay	DB	Soft	DBS	78	2	2
			Hard	DBH	91	2	2
			Rough	DBR	102	2	4
2	Big Gutter	BG	Soft	BGS	121	2	2
			Hard	BGH	118	2	2
			Rough	BGR	113	2	2
	Gabo Reef	GR	Soft	GRS	136	2	2
			Hard	GRH	128	2	2
			Rough	GRR	112	2	2
	The Horseshoe	HO	Soft	HOS	149	2	2
			Hard	HOH	152	2	2
			Rough	HOR	157	2	2

Common name	Species	Trawl	Gill-net

Appendix 4. Checklist of 201 fishes caught during trawl and gill-net surveys of the south-eastern Australian continental shelf
Standardized catches, pooled by survey, shown for four seasonal trawl surveys on soft-sediment substrata (g m^{-2}) and two gill-net surveys on different substrata (kg h^{-1} per net fleet). Commercial species shaded (quota species, dark shade; secondary species, light shade). Common names from Gomon *et al.* (1994) and Last and Stevens (1994), except those marked *; species list arranged phylogenetically according to Yearsley *et al.* (1994). – indicates species not caught

		Early winter	Late winter	Spring	Autumn	Total	Survey 1	Survey 2	Total
Sevengill shark	*Heptranchias perlo*	–	0.002	–	–	0.002	–	–	0.000
Broadnose sevengill shark	*Notorynchus cepedianus*	–	–	0.017	–	0.017	–	–	0.000
Port Jackson shark	*Heterodontus portusjacksoni*	2.679	1.739	4.018	3.411	11.847	46.235	–	46.235
Mako shark	*Isurus oxyrinchus*	–	–	–	–	0.000	1.765	0.391	2.156
Thresher shark	*Alopias vulpinus*	–	–	–	–	0.000	5.575	–	5.575
Rusty carpetshark	*Parascyllium ferrugineum*	0.117	0.084	0.170	0.044	0.416	1.507	–	1.507
Draughtboard shark	*Cephaloscyllium laticeps*	10.097	15.498	8.855	9.650	44.101	114.935	13.935	128.870
Sawtail shark	*Galeus boardmani*	0.067	0.042	0.094	0.056	0.259	–	–	0.000
Whitefin swellshark	*Cephaloscyllium* sp A	0.216	–	1.057	0.018	1.290	–	–	0.000
Dwarf catshark	*Asymbolus* sp A	0.008	–	–	–	0.008	–	–	0.000
Orange-spotted catshark	*Asymbolus* sp D	0.368	0.733	0.552	0.719	2.373	3.111	5.406	8.517
Grey spotted catshark	*Asymbolus analis*	0.154	0.381	1.693	0.397	2.624	0.188	1.346	1.534
Northern draughtboard shark	*Cephaloscyllium* sp C	0.357	–	–	–	0.357	–	–	0.000
Gummy shark	*Mustelus antarcticus*	6.040	1.290	0.305	0.547	8.182	63.988	1.512	65.500
School shark	*Galeorhinus galeus*	0.946	–	0.031	0.035	1.012	5.566	–	5.566
Smooth hammerhead	*Sphyrna zygaena*	–	–	–	0.279	0.279	1.231	–	1.231
Piked spurdog	*Squalus megalops*	3.532	7.304	2.098	2.573	15.506	12.934	167.180	180.114
Southern dogfish	*Centrophorus uyato*	–	–	–	–	0.000	–	0.843	0.843
Southern sawshark	*Pristiophorus nudipinnis*	1.099	0.643	–	0.086	1.828	3.135	–	3.135
Common sawshark	*Pristiophorus cirratus*	2.239	0.398	0.979	0.181	3.798	–	0.832	0.832
Eastern sawshark	*Pristiophorus* sp A	–	0.128	–	0.029	0.158	0.070	1.996	2.066
Australian angel shark	*Squatina australis*	1.640	2.753	0.993	2.998	8.384	–	–	0.000
Eastern angel shark	*Squatina* sp A	0.605	0.194	0.167	–	0.966	–	–	0.000
Western shovelnose ray	*Aptychotrema vincentiana*	0.017	–	–	–	0.017	–	–	0.000
Southern fiddler ray	*Trygonorrhina fasciata*	1.697	–	0.066	0.868	2.630	–	–	0.000
Eastern fiddler ray	*Trygonorrhina* sp A	0.778	1.192	0.280	1.322	3.573	–	–	0.000
Eastern shovelnose ray	*Aptychotrema rostrata*	–	–	–	0.075	0.075	–	–	0.000
Coffin ray	*Hypnos monopterygium*	–	–	–	0.026	0.026	–	–	0.000
Tasmanian numbfish	*Narcine tasmaniensis*	0.358	0.116	0.307	0.578	1.359	–	–	0.000
Short-tail torpedo ray	*Torpedo macneilli*	–	–	–	0.371	0.371	–	–	0.000
Sydney skate	*Raja australis*	–	–	0.266	0.073	0.340	–	–	0.000
Longnose skate	*Raja* sp A	2.373	4.645	2.732	2.804	12.555	–	0.239	0.239
Melbourne skake	*Raja whitleyi*	0.282	2.646	4.803	2.347	10.078	–	–	0.000
Peacock skate	*Pavoraja nitida*	0.064	0.132	0.165	0.164	0.525	–	–	0.000
Bight skate	*Raja gudgeri*	–	0.403	–	–	0.403	–	–	0.000
Smooth stingray	*Dasyatis brevicaudata*	0.347	0.032	0.629	1.448	2.456	–	–	0.000
Black stingray	*Dasyatis thetidis*	–	–	–	1.381	1.381	–	–	0.000
Sandyback stingaree	*Urolophus bucculentus*	3.162	5.425	1.902	2.527	13.017	–	–	0.000
Banded stingaree	*Urolophus cruciatus*	1.179	1.588	3.696	1.361	7.824	0.017	–	0.017
Sparsely-spotted stingaree	*Urolophus paucimaculatus*	5.161	7.798	8.018	5.896	26.872	–	–	0.000
Common stingaree	*Trygonoptera testacea*	–	0.209	–	–	0.209	–	–	0.000
Greenback stingaree	*Urolophus viridis*	3.903	2.674	1.813	2.141	10.531	0.028	–	0.028
Eastern shovelnose stingaree	*Trygonoptera* sp B	0.212	1.083	0.524	3.633	5.452	–	–	0.000
Western shovelnose stingaree	*Trygonoptera mucosa*	0.306	–	–	–	0.306	–	–	0.000
Kapala stingaree	*Urolophus* sp A	0.768	0.783	0.018	0.156	1.724	–	–	0.000
Coral sea stingaree	*Urolophus* sp B	0.521	–	–	–	0.521	–	–	0.000
Southern eagle ray	*Myliobatis australis*	0.629	1.431	4.016	6.839	12.915	–	–	0.000
Ogilbys ghostshark	*Hydrolagus ogilbyi*	0.032	–	1.435	0.266	1.733	–	–	0.000
Blackfin ghostshark	*Hydrolagus lemures*	0.052	0.196	–	–	0.248	–	–	0.000
Elephantfish	*Callorhinchus milii*	0.262	0.190	0.724	0.872	2.048	1.029	–	1.029

Appendix 4 contd over

Appendix 4. *contd*

Common name	Species	Trawl					Gill-net		
		Early winter	Late winter	Spring	Autumn	Total	Survey 1	Survey 2	Total
Pike eel	*Muraenesox bagio*	0.359	–	–	–	0.359	–	–	0.000
Swollenhead conger	*Bassanago bulbiceps*	0.041	–	0.021	–	0.063	–	–	0.000
Giant snake eel	*Ophisurus serpens*	–	–	0.011	–	0.011	–	0.444	0.444
Silverside	*Argentina australiae*	0.002	0.001	0.004	0.004	0.011	–	–	0.000
Sergeant Baker	*Aulopus purpurissatus*	0.003	–	0.046	0.031	0.080	0.628	–	0.628
Cucumberfish	*Chlorophthalmus nigripinnis*	6.290	10.834	12.667	7.110	36.902	–	0.284	0.284
Largescale new lanternfish	*Neoscopelus macrolepidotus*	–	0.029	–	–	0.029	–	–	0.000
Beaked salmon	*Gonorynchus greyi*	0.006	0.002	–	0.009	0.017	–	–	0.000
Coffinfish	*Chaunax endeavouri*	0.114	0.046	–	0.012	0.172	–	–	0.000
Bearded rock cod	*Pseudophycis barbata*	–	–	–	–	0.000	0.841	0.503	1.343
Largetooth beardie	*Lotella rhacinus*	–	–	–	–	0.000	0.049	0.000	0.049
Red cod	*Pseudophycis bachus*	0.252	0.315	0.147	0.723	1.437	1.577	3.438	5.015
Bastard red cod	*Pseudophycis breviuscula*	0.017	–	–	–	0.017	–	–	0.000
Blue grenadier	*Macruronus novaezelandiae*	–	–	0.133	0.040	0.173	–	1.149	1.149
Pink ling	*Genypterus blacodes*	0.564	0.237	0.687	0.663	2.152	0.570	26.376	26.946
Southern whiptail	*Caelorinchus australis*	–	0.143	0.661	0.079	0.884	–	0.036	0.036
Banded whiptail	*Caelorinchus fasciatus*	0.147	–	–	–	0.147	–	–	0.000
Gargoylefish	*Caelorinchus mirus*	0.378	0.261	0.192	0.156	0.988	–	0.028	0.028
Toothed whiptail	*Lepidorhynchus denticulatus*	0.000	–	0.276	0.004	0.281	–	–	0.000
Small banded whiptail	*Caelorinchus parvifasciatus*	0.002	–	–	–	0.002	–	–	0.000
Redfish	*Centroberyx affinis*	51.710	10.588	12.755	22.052	97.105	0.716	6.552	7.268
Swallowtail	*Centroberyx lineatus*	–	0.009	–	–	0.009	0.414	–	0.414
Silver dory	*Cyttus australis*	0.384	1.186	3.262	2.188	7.019	0.104	0.267	0.371
Mirror dory	*Zenopsis nebulosus*	0.028	0.462	1.050	1.442	2.982	–	–	0.000
John dory	*Zeus faber*	1.460	0.640	0.486	1.037	3.623	–	0.114	0.114
New Zealand Dory	*Cyttus novaezelandiae*	0.115	0.241	0.811	0.273	1.440	–	–	0.000
Flutemouth	*Fistularia petimba*	0.001	–	–	–	0.001	–	–	0.000
Banded bellowsfish	*Centriscops humerosus*	–	–	0.015	–	0.015	–	–	0.000
Common snipefish	*Macroramphosus scolopax*	0.928	3.019	2.939	2.657	9.543	–	–	0.000
Crested bellowsfish	*Notopogon lilliei*	–	–	–	0.001	0.001	–	–	0.000
Bigbelly seahorse	*Hippocampus abdominalis*	0.000	0.000	–	0.000	0.001	–	–	0.000
Spiny pipehorse	*Solegnathus spinosissimus*	0.012	0.006	0.007	0.002	0.027	–	–	0.000
Ocean perch	*Helicolenus percoides*	1.762	4.777	5.081	4.490	16.109	1.436	4.559	5.995
Gurnard perch	*Neosebastes pandus*	0.020	–	–	–	0.020	–	–	0.000
Ruddy gurnard perch	*Neosebastes scorpaenoides*	0.046	0.932	3.517	1.897	6.392	0.405	–	0.405
Thetis fish	*Neosebastes thetidis*	0.211	0.055	0.011	0.051	0.330	–	0.123	0.123
Southern rock cod	*Scorpaena papillosa*	0.356	0.227	1.497	0.505	2.586	0.032	0.022	0.054
Western gurnard perch	*Neosebastes entaxis*	0.027	–	–	0.010	0.037	–	–	0.000
Soldierfish	*Gymnapistes marmoratus*	0.553	–	–	–	0.553	–	–	0.000
Northern gurnard perch	*Neosebastes incisipinnis*	–	0.011	0.076	0.015	0.101	–	–	0.000
Whitleys scorpionfish	*Maxillicosta whitleyi*	0.013	0.001	0.002	0.008	0.025	–	–	0.000
Fortesque	*Centropogon australis*	0.003	–	–	0.001	0.004	–	–	0.000
Red rock cod	*Scorpaena cardinalis*	0.001	0.204	0.316	0.017	0.537	–	–	0.000
Deep ocean perch	*Helicolenus barathri*	–	–	1.388	0.296	1.683	–	–	0.000
Red gurnard	*Chelidonichthys kumu*	0.832	0.730	0.440	0.566	2.568	0.147	–	0.147
Spiny gurnard	*Lepidotrigla papilio*	0.010	0.000	0.001	0.001	0.013	–	–	0.000
Butterfly gurnard	*Lepidotrigla vanessa*	0.254	0.519	0.278	0.346	1.396	–	–	0.000
Painted latchet	*Pterygotrigla andertoni*	0.060	0.036	0.252	0.048	0.396	–	–	0.000
Latchet	*Pterygotrigla polyommata*	1.094	0.285	0.127	0.082	1.588	0.050	0.999	1.049
Minor gurnard	*Lepidotrigla modesta*	1.578	2.241	1.677	2.041	7.538	–	0.030	0.030
Deepwater gurnard	*Lepidotrigla mulhalli*	5.410	2.450	1.663	1.313	10.836	0.123	–	0.123
Little red gurnard	*Lepidotrigla grandis*	–	0.035	–	–	0.035	–	–	0.000

Appendix 4 contd over

Appendix 4. *contd*

Common name	Species	Trawl					Gill-net		
		Early winter	Late winter	Spring	Autumn	Total	Survey 1	Survey 2	Total
Crocodilefish	*Satyrichthys lingi*	–	0.073	0.026	–	0.099	–	–	0.000
Tiger flathead	*Neoplatycephalus richardsoni*	7.191	4.187	2.923	3.129	17.431	2.116	18.321	20.437
Sand flathead	*Platycephalus bassensis*	1.387	0.207	0.934	0.108	2.635	0.112	–	0.112
Blue-spotted flathead	*Platycephalus caeruleopunctatus*	–	0.052	0.044	0.045	0.141	–	–	0.000
Northern sand flathead	*Platycephalus arenarius*	0.008	–	–	–	0.008	–	–	0.000
Toothy flathead	*Neoplatycephalus aurimaculatus*	0.049	0.034	0.386	0.062	0.531	–	–	0.000
Long-spined flathead	*Platycephalus longispinis*	0.020	0.037	0.025	0.052	0.135	–	–	0.000
Yank flathead	*Platycephalus speculator*	0.020	–	0.065	0.032	0.118	0.279	–	0.279
Deepsea flathead	*Hoplichthys haswelli*	0.084	0.082	0.284	0.146	0.595	–	0.029	0.029
Eastern orange perch	*Lepidoperca pulchella*	0.035	0.391	0.849	–	1.276	0.080	0.752	0.832
Butterfly perch	*Caesioperca lepidoptera*	–	0.856	0.848	0.070	1.774	3.366	2.176	5.541
Barber perch	*Caesioperca rasor*	0.000	0.038	0.171	2.326	2.536	0.012	–	0.012
Hapuku	*Polyprion oxygeneios*	–	–	–	0.046	0.046	–	1.027	1.027
Halfbanded seaperch	*Hypoplectrodes maccullochi*	–	–	–	–	0.000	0.039	–	0.039
Threespine cardinalfish	*Apogonops anomalus*	1.873	8.228	27.631	12.696	50.428	–	–	0.000
Splendid perch	*Callanthias australis*	–	0.008	0.001	0.011	0.020	0.147	–	0.147
Blackbanded seaperch	*Hypoplectrodes annulata*	–	–	–	–	0.000	0.018	–	0.018
Bigeye	*Cookeolus japonicus*	–	–	–	0.001	0.001	–	–	0.000
Longfin pike	*Dinolestes lewini*	–	0.370	0.029	–	0.399	0.605	–	0.605
King George whiting	*Sillaginodes punctata*	–	–	–	0.011	0.011	–	–	0.000
Eastern school whiting	*Sillago flindersi*	17.095	2.773	6.021	2.704	28.593	0.009	–	0.009
Jack mackerel	*Trachurus declivis*	144.303	61.466	26.864	13.654	246.288	32.468	118.903	151.371
Yellowtail horse mackerel	*Trachurus novaezelandiae*	0.784	1.107	0.284	1.144	3.318	–	–	0.000
Yellowtail kingfish	*Seriola lalandi*	0.020	–	–	0.052	0.072	0.242	–	0.242
White trevally	*Pseudocaranx dentex*	0.844	1.752	0.393	1.896	4.885	2.461	1.160	3.621
Skipjack trevalley	*Pseudocaranx wrighti*	0.146	0.000	0.002	0.001	0.150	–	–	0.000
Peruvian jack mackerel	*Trachurus murphyi*	–	0.232	0.065	–	0.298	–	1.658	1.658
Redbait	*Emmelichthys nitidus nitidus*	23.156	0.163	0.085	0.026	23.431	0.170	6.836	7.005
Silverbelly	*Parequula melbournensis*	1.292	0.588	2.043	0.983	4.906	–	–	0.000
Snapper	*Pagrus auratus*	0.015	0.044	1.173	0.542	1.774	0.220	–	0.220
Red mullet	*Upeneichthys vlamingii*	0.305	0.132	1.127	1.287	2.851	–	–	0.000
Common bullseye	*Pempheris multiradiata*	–	0.568	0.039	–	0.607	0.251	–	0.251
Slender bullseye	*Parapriacanthus elongatus*	0.002	0.563	–	–	0.564	–	–	0.000
Mado	*Atypichthys strigatus*	–	–	–	–	0.000	0.007	–	0.007
Old wife	*Enoplosus armatus*	–	0.003	0.001	–	0.005	–	–	0.000
Giant boarfish	*Paristiopterus labiosus*	–	0.006	0.021	0.013	0.039	0.145	–	0.145
Longsnout boarfish	*Pentaceropsis recurvirostris*	0.089	0.104	0.686	0.217	1.097	0.035	–	0.035
Longfin boarfish	*Zanclistius elevatus*	0.026	0.024	0.042	0.031	0.123	–	–	0.000
White ear	*Parma microlepis*	–	–	–	–	0.000	0.017	–	0.017
Blue morwong	*Nemadactylus douglasi*	0.211	1.876	0.486	1.533	4.106	5.235	0.967	6.202
Jackass morwong	*Nemadactylus macropterus*	2.817	4.670	11.152	4.067	22.705	4.900	22.866	27.766
Banded morwong	*Cheilodactylus spectabilis*	–	–	–	–	0.000	0.360	–	0.360
Striped trumpeter	*Latris lineata*	–	–	–	0.076	0.076	3.378	1.341	4.719
Bastard trumpeter	*Latridopsis forsteri*	–	0.129	–	0.068	0.197	6.861	0.416	7.277
Shortfin seapike	*Sphyraena novaehollandiae*	0.001	–	–	–	0.001	–	–	0.000
Pigfish*	*Bodianus vulpinus*	–	–	–	0.031	0.031	–	–	0.000
Bluethroat wrasse	*Notolabrus tetricus*	–	–	–	–	0.000	0.848	–	0.848

Appendix 4 contd over

Appendix 4. *contd*

Common name	Species			Trawl				Gill-net	
		Early winter	Late winter	Spring	Autumn	Total	Survey 1	Survey 2	Total
Rosy wrasse	*Pseudolabrus psittaculus*	–	0.002	0.028	0.007	0.037	0.062	–	0.062
Deep pigfish*	*Bodianus* sp.	–	–	0.815	–	0.815	–	–	0.000
Maori wrasse	*Ophthalmolepis lineolata*	–	–	–	–	0.000	0.584	–	0.584
Eastern blue grouper	*Achoerodus viridis*	–	–	–	–	0.000	0.685	–	0.685
Pigfish	*Bodianus* sp. 1	–	–	–	–	0.000	0.230	0.411	0.642
Redband wrasse	*Pseudolabrus biserialis*	–	–	–	0.026	0.026	–	–	0.000
Barred grubfish	*Parapercis allporti*	0.088	0.105	0.174	0.121	0.489	–	0.010	0.010
Grubfish*	*Parapercis binivirgata*	–	–	0.002	–	0.002	–	–	0.000
Bulldog stargazer	*Gnathagnus innotabilis*	0.072	0.018	–	0.017	0.107	–	–	0.000
Fringed stargazer	*Ichthyscopus barbatus*	0.012	–	–	–	0.012	–	–	0.000
Common stargazer	*Kathetostoma laeve*	0.248	0.186	0.517	0.173	1.124	–	–	0.000
Speckled stargazer	*Kathetostoma canaster*	0.795	0.954	0.739	1.293	3.781	–	–	0.000
Common stinkfish	*Foetorepus calauropomus*	4.918	4.211	3.303	3.681	16.113	0.007	–	0.007
Spotted stinkfish	*Repomucenus calcaratus*	–	–	–	0.002	0.002	–	–	0.000
Barracouta	*Thyrsites atun*	6.093	44.627	13.825	2.597	67.143	23.622	19.640	43.262
Gemfish	*Rexea solandri*	0.002	0.123	4.067	1.216	5.408	–	1.941	1.941
Frostfish	*Lepidopus caudatus*	0.011	0.133	0.670	1.019	1.832	–	0.191	0.191
Blue mackerel	*Scomber australasicus*	0.085	0.056	0.323	0.641	1.104	4.783	11.336	16.119
Australian bonito	*Sarda australis*	–	–	–	–	0.000	0.266	–	0.266
Warehou	*Seriolella brama*	2.898	4.665	4.267	0.255	12.085	47.394	21.666	69.060
Spotted trevalla	*Seriolella punctata*	19.514	2.101	0.589	1.965	24.170	–	3.827	3.827
Crested flounder	*Lophonectes gallus*	0.002	–	0.001	0.000	0.003	–	–	0.000
Smalltooth flounder	*Pseudorhombus jenynsii*	–	0.007	–	0.012	0.019	–	–	0.000
Longsnout flounder	*Ammotretis rostratus*	0.044	0.009	0.042	0.042	0.137	–	–	0.000
Bandedfin flounder	*Azygopus pinnifasciatus*	0.002	–	–	0.005	0.007	–	–	0.000
Greenback flounder	*Rhombosolea tapirina*	0.013	0.032	0.013	0.003	0.061	–	–	0.000
Manybanded sole	*Zebrias scalarias*	0.002	–	–	–	0.002	–	–	0.000
Toothbrush leatherjacket	*Acanthaluteres vittiger*	0.056	0.016	0.056	0.092	0.220	–	–	0.000
Mosaic leatherjacket	*Eubalichthys mosaicus*	0.227	0.125	0.416	0.441	1.208	0.486	–	0.486
Velvet leatherjacket	*Meuschenia scaber*	1.870	12.201	7.420	5.473	26.964	0.665	0.060	0.725
Chinaman leatherjacket	*Nelusetta ayraudi*	0.003	–	0.019	0.013	0.036	–	–	0.000
Rough leatherjacket	*Scobinichthys granulatus*	–	–	–	0.006	0.006	–	–	0.000
Brownstriped leatherjacket	*Meuschenia australis*	0.003	–	–	0.021	0.024	–	–	0.000
Little leatherjacket*	*Paramonacanthus filicauda*	–	–	–	0.572	0.572	–	–	0.000
Southern pygmy leatherjacket	*Brachaluteres jacksonianus*	0.001	–	–	–	0.001	–	–	0.000
Sixspine leatherjacket	*Meuschenia freycineti*	0.333	1.220	0.758	0.175	2.485	0.137	–	0.137
Degens leatherjacket	*Thamnaconus degeni*	0.549	0.634	5.063	2.702	8.947	0.015	–	0.015
Black reef leatherjacket	*Eubalichthys bucephalus*	0.004	0.007	0.018	–	0.029	–	–	0.000
Stars-and-stripes leatherjacket	*Meuschenia venusta*	–	–	0.037	–	0.037	–	–	0.000
Ornate cowfish	*Aracana ornata*	0.011	0.005	–	–	0.017	–	–	0.000
Eastern smooth boxfish	*Anoplocapros inermis*	0.036	0.186	0.214	0.310	0.746	–	–	0.000
Shaws cowfish	*Aracana aurita*	0.022	0.034	0.184	0.157	0.397	–	–	0.000
Barred toadfish	*Contusus richei*	0.353	0.012	0.658	0.029	1.052	–	–	0.000
Ringed toadfish	*Omegophora armilla*	0.002	–	–	0.047	0.049	–	–	0.000
Pufferfish*	*Sphoeroides pachygaster*	0.007	0.026	–	0.003	0.036	–	–	0.000
Starry toadfish	*Arothron firmamentum*	–	–	–	1.134	1.134	–	–	0.000
Halstead's toadfish	*Reicheltia halsteadi*	0.001	–	–	–	0.001	–	–	0.000
Globefish	*Diodon nicthemerus*	2.562	2.259	4.444	2.145	11.410	–	–	0.000
Australian burrfish	*Allomycterus pilatus*	1.446	4.050	0.862	1.515	7.872	–	–	0.000
--	Not identified 3	–	–	0.005	–	0.005	–	–	0.000
--	Not identified 2	–	–	0.004	–	0.004	–	–	0.000
--	Not identified 1	–	–	0.002	–	0.002	–	–	0.000
	Total	371.456	271.026	239.265	181.526		411.721	474.853	

Mar. Freshwater Res., 2001, **52**, 537–48

Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf

C. Bulman, F. Althaus, X. He, N. J. Bax and A. Williams

CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia

Abstract. A total of 8200 stomach samples was collected from 102 fish species caught by trawl or gillnet during research surveys on the south-eastern Australian shelf from 1993 to 1996. Diet compositions were analysed based on percentages of wet weight of prey. Of the total fish examined, 70 species had sufficient stomach samples (i.e. >10) for further analysis. Ten trophic guilds were identified from cluster analysis. Benthic prey dominated the diets. However, analysis on a subset of 28 abundant species that were commercially and ecologically important, showed that pelagic prey was dominant, particularly for 12 quota species. This suggests that pelagic production contributes significantly to the trawl fishery production. Further analysis on the diets of these 28 species found that although fish was more important than invertebrate prey, there was no evidence of significant predation on commercially important species (quota species) by other fish species. A food web diagram was constructed, mostly based on the diet compositions, guild structure and relative abundance of commercially and ecologically important fish species, to show major trophic interactions of the shelf ecosystem.

Introduction

The south-eastern Australian shelf, off Victoria and New South Wales (NSW) (Fig. 1), has been supporting demersal fisheries since the early 1900s (Tilzey 1994). Over 22 species are being harvested, with average annual fishery landings of ~25000 t (Tilzey 1999). However, ecological interactions among these harvested species and between the harvested species and other abundant species have not been well studied. Since most fish are harvested by demersal trawls, we initially believed that benthic production would be the most important contribution to fishery production, whereas pelagic contributions, from either on or off the shelf, were believed to be relatively minor. Also, predation on harvested species, which could provide additional information on relative importance of fishing effects on the demersal fish communities, is poorly understood.

Between 1993 and 1997, CSIRO Marine Research conducted intensive investigations of factors that affect fishery production on the south-eastern Australian shelf (Bax *et al.* 1999; Bax and Williams 2000; Williams and Bax 2001). The project was multi-faceted and investigated the association of fish assemblages with habitats, and the influences of physical and chemical variables of the habitat in the biological attributes of the assemblages (papers in this issue). This paper presents the major parts of the project results on the diets and trophic guilds of commercially and other abundant or potentially piscivorous fish species. Specifically, the aims of this study were: (1) to describe the diets of ecologically and commercially important fish species in the shelf; (2) to identify the trophic guild structure of the fish community; (3) to compare the relative importance of pelagic and benthic contributions to the fishery production by comparing pelagic and benthic prey sources of commercial species; and (4) to evaluate the magnitude of predation on commercially important (quota) species. A conceptual food web model was also constructed, based on the diet compositions and the guild structure of the

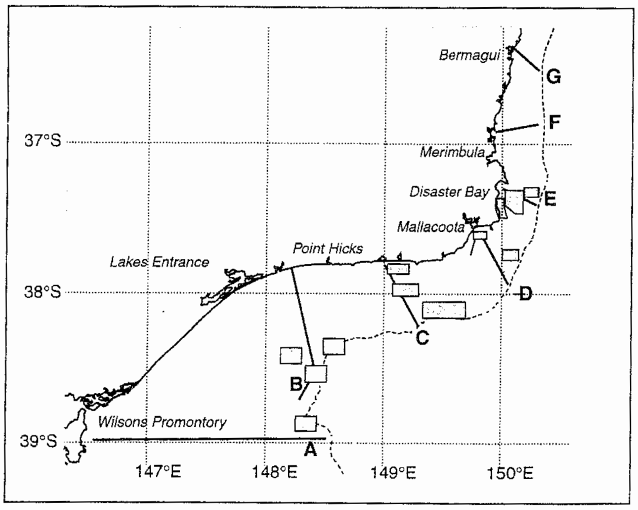


Fig. 1. Map of study area off south-eastern Australia, showing locations of transects A–G (bold lines) and mesohabitat study areas (greyed boxes).

10.1071/MF99152 1323-1650/01/040537

important species, to illustrate important trophic interactions in the shelf.

Methods

Study area

The study area was from Wilsons Promontory on the southern Victorian coast to Bermagui on the NSW coast in the south-eastern Australia continental shelf. The total area represented was about 23 900 km^2 within a depth range of 40–200 m. The sampling design had two phases: broad scale surveys and focussed area surveys. For the broad scale surveys, seven transects were sampled, each transect consisting of stations spaced at 25 m, 40 m, 80 m, 120 m and 200 m depths across the shelf (Fig. 1). For the focussed area surveys, sampling was focussed within six study areas or mesohabitats. Within these mesohabitats, 17 macrohabitats were defined at a finer scale. Details of the sampling locations and strategies are described in Bax and Williams 2000 and other papers (this volume). Fish were caught by bottom trawls in the broad scale surveys or by traps or gillnets in the focussed area surveys. Only data from the bottom trawls and gillnets were used in the analysis because trapped fish would have eaten bait. Data from the broad scale surveys and the focussed area surveys are combined in the analysis.

Sample collections

Surveys were conducted on the FRV *Southern Surveyor* during July–August 1993 (winter), August–September 1994 (spring), April–May 1996 (autumn) and November–December 1996 (summer), to cover seasons. Collections were made throughout each survey for the broad scale and focussed area studies. Where possible, a range of depths, time, geographical locations and size of fish was sampled for each species. From each bottom trawl, stomachs were removed from up to 10 fish per selected species. Fish that were obviously net-feeding were not selected. A maximum of 50 stomachs per species per cruise was taken. Additional samples were collected during commercial boat surveys in macrohabitats with non-trawl gear during June through October 1994, September 1995, May 1996 and January 1997. Large stomachs were frozen at –20°C and small stomachs were preserved in 10% formalin. Biological details such as length, weight and sex of sampled fish were recorded.

In the laboratory, stomachs were assessed for fullness and then dissected. Prey items were identified to the lowest possible taxon. Items were counted, blotted on absorbent paper to remove excess moisture and weighed (to 0.001 g in the case of very small items). Fish digested beyond recognition were identified from otoliths if possible. Squid beaks were identified by Dr C. C. Lu (formerly Museum of Victoria). No attempts were made to back-calculate sizes of animals from otolith or beak sizes.

Diets were described by determining the proportions of prey by wet weight in stomachs containing food, as this best represented trophic flows. Prey items were aggregated to 14 categories for further analyses. The functional categories were generally based on taxonomy and primary habitat except in the case of megabenthos that comprised two phyla, Mollusca and Crustacea. A similar system was used by Fujita *et al.* (1995) when examining shelf fishes off northern Japan. Justification for categorization was drawn from references such as Last *et al.* (1983), Bulman and Blaber (1986), Blaber and Bulman (1987), Gomon *et al.* (1994), Jones and Morgan (1994) and personal communication with CSIRO colleagues. Since over 800 prey items were identified, only the major taxa comprising the functional categories are listed in Table 1. Some taxa may comprise species that are categorized in different functional groups, e.g. Caridea, Ascidiacea, Macrouridae.

Data analysis

Overall, 217 species were caught during these surveys and stomachs were taken from 102 species (Bax *et al.* 2000). From this total, we chose 70 species for analysis because we were able to take sufficient numbers of stomach samples, usually more than 10 (Table 2). Initial analysis showed that sample variability was high between and within samples for some species. Therefore, all samples for a species were amalgamated in the analysis to represent an overall diet composition.

A cluster analysis was used to classify the 70 species into groups, which we assumed to represent trophic guilds. In the cluster analysis, the three unknown prey categories—fish, invertebrate and crustacean—were pro-rated across the appropriate prey categories to maximize the data available for use in the cluster analyses. We

Table 1. Functional prey categories and major prey taxa used to aggregate prey data in diet analyses of 70 fish species from the south-eastern Australian shelf

Species were identified from the taxa listed. Note that some taxa occur in more than one functional group

Functional group	Major taxa comprising functional groups
Benthic invertebrates	Echinodermata, Ascidiacea, Ectoprocta, Cnidaria, Branchiopoda, Gastropoda, Porifera, Sipuncula, Platyhelminthe, Echiura
Polychaetes	Polychaeta
Benthic crustaceans	Isopoda, Caprellidae, Gammaridae, Cyclopoida, Harpacticoida, Cumacea, Ostracoda, Stomatopoda
Megabenthos	Anomura, Brachyura, Homolidae, Caridea, Octopoda, Sepioida
Benthic fish	Bothidae, Callionymidae, Congridae, Elasmobranchii, Gerreidae, Gobiesocidae, Gonarynchidae, Macrorhamphosidae, Monacanthidae, Moridae, Opichthidae, Ophidiidae, Pempheridae, Pinguipedidae, Platycephalidae, Pleuronectidae, Rajidae, Scorpaenidae, Sillaginidae, Syngnathidae, Triglidae
Benthopelagic fish	Berycidae, Carangidae, Chlorophthalmidae, Gempylidae, Macrouridae, Ophididae, Percichthyidae, Platycephalidae, Scorpaenidae, Serranidae, Trichiuridae, Zeidae
Pelagic fish	Argentinidae, Congridae, Emmelichthyidae, Idiacanthidae, Malacosteidae, Myctophidae, Phosichthyidae, Scombridae, Scorpaenidae, Sternoptychidae
Pelagic invertebrates	Ascidiacea, Thaliacea, Teuthoidea, Nautiloidea, Cnidaria
Pelagic crustaceans	Penaeidae, Sergestidae, Caridea, Euphausiacea, Mysida, Calanoida, Cyclopoida, Hyperiidae
Unknown fish	Unidentifiable fish remains
Unknown crustaceans	Unidentifiable crustacean remains
Unknown invertebrates	Unidentifiable invertebrate remains other than crustacean
Unknown	Unidentifiable remains
Other	Sediment, macroalgae, seagrasses

assumed that this method based on the known diet components of the individual species, would best represent their diets. The unknown category was not pro-rated because it could not provide additional information. In the cluster analysis, we used Bray-Curtis dissimilarity coefficients with an average linkage clustering algorithm (SPSS Version 6.1, 1994).

A subset of 28 species was chosen for which we determined the relative importance of benthic and pelagic sources of prey, and the importance of quota fish species as prey. This subset consisted of 12 quota species and a further 16 'important' species (Table 2). We selected important species based on their high relative abundance in our surveys and their high representation in diets of the species analysed. The subset contributed between 44% and 76% of fish biomass caught in the broad scale trawl surveys, depending on area, and 78% of the biomass caught by trawl from the mesohabitat sites (see Bax *et al.* 2000 for more detail). Benthopelagic prey were classed as pelagic sources for this analysis as our diet data showed that for many species, most of their food was pelagic.

A food web was constructed for the shelf ecosystem. This will serve as a conceptual model for the trophic interactions of the system. We based the food web on the diet data and derived guild structure from the analysis, relative abundance of species and importance to the commercial fisheries in the shelf system. The model emphasized details in fish species with simplified components in the low trophic levels (plankton and benthic invertebrates). It does not include higher trophic levels such as seals, birds, tuna or large pelagic sharks.

Results

General description

Of the 70 species, about one-third was piscivorous (Table 3). Within families, diets could vary markedly between species. For example, in the dory family, three of the four dories were piscivores, *Zeus faber*, *Zenopsis nebulosus* and *Cyttus australis*, whereas *Cyttus novaezelandiae* ate only pelagic crustaceans. In the Triglidae, three species, *Chelidonichthys kumu*, *Lepidotrigla vanessa* and *Pterygotrigla polyommata* ate mainly benthic fish whereas the two others were invertebrate feeders: *Lepidotrigla mulhalli* was a benthopelagic feeder and *Lepidotrigla modesta* was a benthic feeder. In the *Caelorinchus* species, *C. mirus* was a benthic piscivore, *C. australis* was an omnivore and *C. parvifasciatus* and *C. fasciatus* were polychaete specialists.

Fish within families used not only very different prey but also different sources i.e. either pelagic or benthic In the Scorpaenidae, both *Helicolenus percoides* and the closely related perch species, *Helicolenus barathri*, ate fish, pyrosomes, crabs, cephalopods and shrimps but the former ate a larger proportion of pelagic prey. In contrast, *Neosebastes scorpaenoides* ate more benthic prey such as crabs, gastropods and benthic fish. In the Serranid family, the *Caesioperca lepidoptera* ate benthic invertebrates such as ascidians, coral and polychaetes and pelagic shrimps, copepods and pyrosomes. In contrast, *Caesioperca rasor* and *Lepidotrigla pulchella* were piscivores, probably benthopelagic, and *Apogonops anomalus* was a pelagic piscivore.

Family members might also eat similar prey taxa but from different sources, such as in the previous example of the piscivorous perches. Both flatheads, *Neoplatycephalus richardsoni* and *Platycephalus bassensis*, were piscivores, but the former ate benthopelagic fish whereas the latter ate benthic fish.

Species that foraged in the same part of the water column could use different prey taxa. For example, the pelagic species, *Trachurus declivis* and *T. novaezelandiae*, ate largely myctophids and euphausiids. Similarly, *Centroberyx affinis* ate predominantly *Apogonops anomalus* and the same euphausiids. However, both warehous, *Seriolella* species, ate mostly pyrosomes.

Some species specialized in quite specific prey items; the warehous in pyrosomes, and as an example of exclusive piscivores, *Genypterus blacodes*, *Lepidoperca pulchella* and *Rexea solandri* all ate predominantly fish but from benthic, benthopelagic and pelagic origins, respectively.

Guild structure

Overall diets were calculated, and prey items were amalgamated into the broad prey categories for cluster analysis (Table 3). From the dendrograms the nine guilds produced were identified at a dissimilarity level of 70% (Fig. 2), including a group of species whose diet consisted predominantly of unknown prey. These species probably did not group into more descriptive groups because not enough data were available to describe their diets reliably. A few species could be misappropriately clustered because the reproportioned data might misrepresent their real feeding preferences, i.e. benthic, benthopelagic or pelagic. Also, these data were based on proportions by weight that might overemphasize larger, rarer prey items or underemphasize smaller, more common prey items, and so give a false impression of the guild to which the fish actually belongs.

Omnivores were species that ate a variety of invertebrate prey in dominant proportions and included fish at greater than 10%. Benthopelagic omnivores specializing in megabenthos and benthic crustaceans were *Caelorinchus australis*, *Helicolenus percoides*, *H. barathri*, *Squalus megalops* and *Mustelus antarcticus. Pseudolabrus psittaculus* was probably also a benthopelagic omnivore but ate a high proportion of unknown prey. Also specializing in megabenthos and small crustaceans was a group of epibenthic invertebrate feeders including *Urolophus* species and two benthic omnivores, *Raja* sp. A and *Neosebastes scorpaenoides*. The last two ate fish in low proportions (between 10% and 50%), which may account for why they were not differentiated from the epibenthic invertebrate feeders in the analyses. These two groups differentiated at about 65% dissimilarity.

Polychaete specialists were included invertebrate feeders *Parequula melbournensis* and *Narcine tasmaniensis* and

Table 2. Common and scientific names and numbers of stomach samples for the 70 fish species from the south-eastern Australian shelf

The list is divided into three parts: 12 quota species (commercial fishery); 16 ecologically important species (abundant species); and the remaining 32 species. The species in the first two parts comprise the subset used in detailed analyses

Species name	Common name	No. stomachs containing food	No. stomachs examined
Quota species			
Centroberyx affinis	Redfish	379	485
Genypterus blacodes	Pink ling	93	111
Helicolenus percoides	Ocean perch	572	848
Nemadactylus macropterus	Jackass morwong	327	552
Neoplatycephalus richardsoni	Tiger flathead	171	350
Pseudocaranx dentex	White trevally	27	72
Rexea solandri	Gemfish	6	12
Seriolella brama	Blue warehou	80	130
Seriolella punctata	Silver warehou	283	462
Sillago flindersi	Eastern school whiting	52	222
Zenopsis nebulosus	Mirror dory	19	59
Zeus faber	John dory	120	29
Ecologically important species			
Apogonops anomalus	Three-spined cardinal fish	79	115
Caesioperca lepidoptera	Butterfly perch	53	65
Cephaloscyllium laticeps	Draughtboard shark	93	14
Chlorophthalmus nigripinnis	Cucumberfish	210	242
Cyttus australis	Silver dory	103	149
Lepidotrigla mulhalli	Deepwater gurnard	130	165
Macrorhamphosus scolopax	Common bellowsfish	236	254
Meuschenia scaber	Velvet leatherjacket	66	87
Synchiropus calauropomus	Common stinkfish	121	142
Urolophus paucimaculatus	Sparsely-spotted stingaree	147	154
Helicolenus barathri	Deep ocean perch	54	74
Latris lineata	Striped trumpeter	12	22
Nemadactylus douglasi	Grey morwong	19	22
Platycephalus bassensis	Sand flathead	13	42
Squalus megalops	Spikey dogfish	130	190
Trachurus declivis	Jack mackerel	345	586
Other species			
Allomycterus pilatus	Deepwater burrfish	17	24
Arothron firmamentum	Starry toadfish	11	11
Atypichthys strigatus	Mado sweep	24	31
Azygopus pinnifasciatus	Banded-fin flounder	10	20
Caelorinchus australis	Southern whiptail	24	24
Caelorinchus fasciatus	Banded whiptail	25	36
Caelorinchus mirus	Gargoyle fish	58	58
Caelorinchus parvifasciatus	Faint-banded whiptail	12	13
Caesioperca rasor	Barber perch	11	18
Chelidonichthys kumu	Red gurnard	25	25
Cyttus novaezelandiae	New Zealand dory	40	40
Diodon nicthemerus	Globefish	80	114
Emmelichthys nitidus nitidus	Redbait	78	89
Galeorhinus galeus	School shark	3	12
Kathetostoma canaster	Speckled stargazer	23	23
Kathetostoma laeve	Common stargazer	15	16
Latridopsis forsteri	Bastard trumpeter	20	20
Lepidoperca pulchella	Eastern orange perch	6	25
Lepidotrigla modesta	Minor gurnard	119	129
Lepidotrigla vanessa	Butterfly gurnard	20	20
Meuschenia freycineti	Sixspined leatherjacket	72	72

Mustelus antarcticus	Gummy shark	7	17
Narcine tasmaniensis	Tasmanian numbfish	37	37
Neosebastes scorpaenoides	Ruddy gurnard perch	30	30
Notolabrus tetricus	Bluethroat wrasse	6	9
Ophthalmolepis lineolata	Maori wrasse	11	13
Pagrus auratus	Snapper	13	17
Paramonacanthus filicauda	Leatherjacket	9	10
Parequula melbournensis	Silverbelly	10	10
Parma microlepis	White ear	1	5
Pempheris multiradiatus	Common bullseye	10	26
Pseudolabrus psittaculus	Rosy wrasse	12	14
Pterygotrigla polyommata	Latchet	20	22
Raja sp. A	Longnose skate	63	63
Scomber australasicus	Blue mackerel	48	59
Scorpis lineolata	Silver sweep	8	8
Squatina australis	Australian angel shark	37	47
Thyrsites atun	Barracouta	174	24
Trachurus novaezelandiae	Yellowtail horse mackerel	10	10
Urolophus cruciatus	Banded stingaree	132	132
Urolophus sp. A	Kapala stingaree	7	7
Urolophus viridis	Green-back stingaree	120	120

also benthic omnivores *S. flindersi* and *Nemadactylus macropterus*.

Meuschenia freycineti, *Meuschenia scaber* and *Synchiropus calauropomus* were included in the group of epibenthic invertebrate feeders and omnivores that ate invertebrates other than crustaceans.

The groups containing the benthic and benthopelagic piscivores clearly differentiated in the dendrogram grouping. These groups ate more than 50% fish, and in most cases more than 80%. *Zeus faber*, *Zenopsis nebulosus*, *Pagrus auratus*, *Kathetostoma laeve*, *Thyrsites atun*, *Galeorhinus galeus* and *Neoplatycephalus richardsoni* were virtually exclusive piscivores.

Pelagic invertebrate feeders, *Seriolella punctata* and *S. brama*, fed mostly on pyrosomes. *Cyttus novaezelandiae* and *Paramonacanthus filicauda* and *Pempheris multiradiata* were pelagic crustacean feeders, whereas *Trachurus declivis* and *Centroberyx affinis* included fish in their diets, and were classified as omnivores.

Apogonops anomalus and *Scorpis lineolata* were pelagic piscivores. *Scomber australasicus* also clustered as a piscivore but might be better classified as a pelagic omnivore since it ate mostly pelagic invertebrates such as ascidians, pyrosomes and salps and less than 40% fish.

Prey sources

In the full data set of 70 species, more than half the species, i.e. 37, relied on benthic foods as their major food source. In contrast, pelagic prey sources dominated in 18 of the 28 commercial or abundant species (Plate I). Furthermore, the diets of nine of the 12 quota species, i.e. *R. solandri*, *Z. nebulosus*, *S. brama*, *S. punctata*, *C. affinis*, *Z. faber*, *P. dentex*, *H. percoides* and *N. richardsoni*, were dominated by pelagic prey sources. The species that ate predominantly benthic prey were *S. flindersi*, *N. macropterus*, *G. blacodes*, *L. mulhalli*, *U. paucimaculatus*, *H. barathri*, *M. scaber*, *P. bassensis*, *S. calauropomus* and *N. douglasi*, of which the first three were quota species. Prey of *M. scolopax* was largely unidentified (70%) but likely to have also been benthic.

Piscivory on quota species

The majority of the 28 commercial or abundant species were piscivorous. Fish comprised more than 50% of the diets of 12 species and more than 30% of 15 species (Table 4). However, of all the fish-eaters, 27 of the 28 species, only four ate more than 1% of quota species. The highest proportions were found in the diets of *L. lineata* where 17% of the diet was *Helicolenus* species and in *Z. faber* where 10% of the diet was *C. affinis*. *N. richardsoni* ate over 5% of *S. flindersi* and 2% of *G. blacodes*. Also of interest was that *T. declivis*, a non-quota species, was eaten in large amounts by *Z. faber* (43%), *Z. nebulosus* (50%) and *C. laticeps* (34%).

Food web

In the food web diagram (Fig. 3), the 70 fish species were grouped into 16 trophic boxes. These groupings were largely based on the diet compositions (Table 3), similarities of life history and growth patterns, importance to the commercial fisheries and ecological importance (relative abundance). The groupings, however, were very arbitrary. All fish boxes, except the small fishes one, were intended to represent interactions between adult or subadult fishes. Juvenile fishes were pooled in the small fish box. The additional six prey categories were added to represent major prey groups for both benthic and pelagic prey sources. Arrows connecting boxes represent major food web

Table 3. Diets of fish from the south-eastern Australian shelf expressed as percentage by weight for 14 prey categories
See text for details of each prey category (* denotes <1% and – denotes prey is absent)

Predator	Other	Benthic invertebrate	Polychaeta	Benthic crustacean	Megabenthos	Benthic fish	Benthopelagic fish	Pelagic invertebrate	Pelagic crustacean	Pelagic fish	Unknown invertebrate	Unknown crustacean	Unknown fish	Unknown
Quota species														
Centroberyx affinis	*	*	*	2	5	2	26	*	35	7	–	20	3	*
Genypterus blacodes	*	2	*	*	9	69	9	7	1	*	*	*	2	*
Helicolenus percoides	*	2	1	8	9	21	9	32	1	2	–	1	13	1
Nemadactylus macropterus	*	5	43	11	7	1	5	1	9	*	–	5	5	8
Neoplatycephalus richardsoni	*	*	*	1	2	39	23	*	*	16	–	1	18	–
Pseudocaranx dentex	–	*	*	5	9	*	60	–	*	–	–	*	*	25
Rexea solandri	–	–	–	–	–	–	15	–	–	–	–	–	79	6
Seriolella brama	*	*	*	*	–	*	–	71	*	–	11	*	*	16
Seriolella punctata	*	*	*	*	*	–	–	83	*	–	–	*	*	16
Sillago flindersi	–	18	45	1	1	3	–	1	*	–	1	1	23	7
Zenopsis nebulosus	–	–	–	–	*	–	51	–	–	45	–	–	3	*
Zeus faber	*	*	*	*	*	11	67	2	*	10	–	*	11	–
Ecologically important species														
Apogonops anomalus	*	–	*	–	1	–	–	*	12	23	–	3	60	1
Caesioperca lepidoptera	–	3	*	*	*	–	–	41	4	–	–	5	*	46
Cephaloscyllium laticeps	*	4	*	*	28	5	42	6	–	1	–	2	11	–
Chlorophthalmus nigripinnis	3	7	3	2	10	1	–	24	21	–	3	7	8	11
Cyttus australis	*	*	–	*	1	40	48	*	4	–	–	1	5	*
Lepidotrigla mulhalli	–	1	*	20	25	*	–	*	28	–	–	23	1	1
Macrorhamphosus scolopax	3	4	4	15	3	*	–	1	3	–	*	52	*	14
Meuschenia scaber	5	58	3	*	2	–	–	2	*	–	*	1	–	29
Synchiropus calauropomus	26	38	7	2	9	–	–	*	*	–	*	8	*	11
Urolophus paucimaculatus	*	3	17	7	27	*	–	*	1	–	–	38	*	7
Helicolenus barathri	*	8	12	21	9	5	4	5	5	1	–	7	19	3
Latris lineata	–	2	–	*	*	28	45	4	–	–	–	–	20	–
Nemadactylus douglasi	*	2	3	3	82	–	–	–	*	–	–	1	5	3
Platycephalus bassensis	–	1	*	–	1	66	–	6	–	–	–	–	25	–
Squalus megalops	–	4	1	*	23	13	10	18	*	*	*	1	28	1
Trachurus declivis	1	1	*	*	*	*	*	1	31	18	–	32	13	2
Other species														
Allomycterus pilatus	–	38	–	20	25	–	–	1	–	–	–	15	*	–
Arothron firmamentum	2	20	3	8	*	–	–	1	13	–	–	19	–	33
Atypichthys strigatus	*	*	–	*	*	*	–	9	*	–	–	*	83	7
Azygopus pinnifasciatus	–	87	8	1	–	–	–	*	–	–	–	1	1	1
Caelorinchus australis	–	*	24	13	25	21	–	9	1	–	–	6	1	–
Caelorinchus fasciatus	–	17	32	5	22	–	–	*	2	–	–	9	*	13
Caelorinchus mirus	–	1	1	5	10	–	–	*	2	–	–	9	59	13
Caelorinchus parvifasciatus	–	36	51	1	5	–	–	–	–	–	–	3	2	3
Caesioperca rasor	–	5	–	*	–	*	–	11	8	–	–	2	70	4
Chelidonichthys kumu	4	3	*	–	1	87	2	1	–	–	–	–	1	*
Cyttus novaezelandiae	–	–	–	–	–	–	–	–	95	–	–	5	–	–
Diodon nicthemerus	*	50	2	8	38	–	–	1	–	–	–	–	–	*
Emmelichthys nitidus nitidus	–	*	–	*	*	–	–	27	18	–	–	14	4	37
Galeorhinus galeus	–	*	–	1	2	7	42	1	–	15	–	*	32	–
Kathetostoma canaster	–	*	–	*	4	16	76	1	–	–	–	–	3	*
Kathetostoma laeve	–	*	–	*	1	44	39	*	–	–	–	*	16	–
Latridopsis forsteri	3	4	1	10	2	–	–	–	–	–	–	6	–	75
Lepidoperca pulchella	–	1	–	–	–	–	–	*	*	–	–	1	98	*

Lepidotrigla modesta	*	*	4	10	63	1	–	–	9	2	–	10	*	*
Lepidotrigla vanessa	–	*	–	*	11	71	–	*	4	–	–	1	13	*
Meuschenia freycineti	2	61	4	3	16	–	*	7	–	–	1	3	1	2
Mustelus antarcticus	–	*	*	1	35	*	9	46	–	–	–	7	2	–
Narcine tasmaniensis	–	12	84	2	1	–	–	–	*	–	1	*	–	1
Neosebastes scorpaenoides	–	23	–	8	50	16	–	*	–	–	–	*	2	–
Notolabrus tetricus	–	41	–	–	18	–	–	29	–	–	–	2	6	5
Ophthalmolepis lineolata	–	18	–	–	6	–	–	–	–	–	–	*	69	6
Pagrus auratus	–	4	–	*	–	7	89	*	–	–	–	*	*	–
Paramonacanthus filicauda	–	1	*	–	–	–	–	*	26	–	–	73	–	*
Parequula melbournensis	–	18	64	4	*	–	–	–	–	–	–	1	–	13
Parma microlepis	*	16	*	–	–	–	–	1	–	–	–	–	–	83
Pempheris multiradiatus	–	–	20	*	*	–	–	*	76	–	–	3	–	1
Pseudolabrus psittaculus	–	32	–	–	–	–	–	–	1	–	–	17	27	23
Pterygotrigla polyommata	–	–	–	–	20	65	3	*	–	–	–	*	12	–
Raja sp. A	*	*	*	1	46	44	*	1	1	–	–	2	4	1
Scomber australasicus	–	*	*	*	–	–	–	35	5	–	–	22	38	1
Scorpis lineolata	*	–	2	–	–	–	–	18	*	–	–	–	80	–
Squatina australis	*	1	*	1	*	20	5	1	*	2	–	*	70	*
Thyrsites atun	–	–	–	*	*	12	64	*	1	4	–	*	19	*
Trachurus novaezelandiae	–	–	–	1	–	–	–	*	8	–	–	1	–	89
Urolophus cruciatus	*	21	42	5	15	–	–	*	*	–	*	9	–	7
Urolophus sp. A	–	*	*	16	57	–	–	–	8	–	–	14	–	4
Urolophus viridis	*	2	16	11	30	*	–	–	3	–	*	30	3	6

interactions. The apex predators appeared to be dogfish (which included small sharks), dories, ling, flathead and a group of large fish including *Chelidonicthys kumu*, *Latris lineata* and *Pagrus auratus* (see Table 2 for scientific or common names).

Discussion

The study of guild structure in community ecology has become popular to illustrate the internal organization of communities (Jaksic and Medel 1990). The term guild has been defined as the ' .. term [which] groups together species, without regard to taxonomic positions, that overlap significantly in their niche requirements' (Root 1967 cited in Jaksic and Medel 1990). Studies of guild structure are generally restricted to single phylogenetic groups, such as the fishes in this study, but they provide basic structures from which further analysis of food web and linkages to other components of ecosystems can be derived. Definition of guild structure is no doubt dependent on aggregations of data, such as prey groupings (see below for more discussion), and on statistical methods used for classifications. We believe that the analysis broadly represented the guild structure of this system.

The guild assignments of species in this study were mostly the same as those determined in other studies in this region. *Apogonops anomalus*, *Genypterus blacodes* and *Helicolenus percoides* were assigned to similar guilds in a study on the upper slope off eastern Tasmania (Blaber and Bulman 1987). On the other hand, we assigned *T. declivis* to the pelagic omnivore guild, whereas Blaber and Bulman (1987) assigned it to the pelagic piscivore guild. The difference here is mainly due to the contribution of fish in diets. In this study, the contribution of fish was 38%, if we converted wet weight to energy terms, compared with 90% energy in the Tasmanian study. If we had used energy terms, we would also have assigned it to the pelagic piscivore group according to our criteria. It is also possible that differences in diet could be due to depth or locality differences. Young *et al.* (1993) and Williams and Pullen (1993) found that the diets of *T. declivis* caught at similar depths to this study were dominated by *Nyctiphanes australis*, a neritic euphausiid known as krill, during autumn. They suggest that *T. declivis* might aggregate when krill is abundant but switch to other abundant prey such as mesopelagic fishes. Similar results were also found in the early slope study (Blaber and Bulman 1987).

In this study, we did not consider the relative abundances of either predators or prey, although their importance can be seen from the *T. declivis* example. Variation in diet could be due to seasonality in predator or prey abundance, ontogenetic shifts in diet, depth and location. Since we did not examine these variations here, the results presented in this paper should be considered as overall averages of diet compositions and guild structure of the system. Detailed descriptions of the diets of these species, as related to fish size, depth and habitat types, are certainly possible and will be analysed further in separate papers.

Although nearly half the fish in the subset of 28 species were highly piscivorous—more than 50% of their diet was fish—very little of the fish component comprised quota species. However, it is not known if a significant portion of the unidentified fish component might have been quota

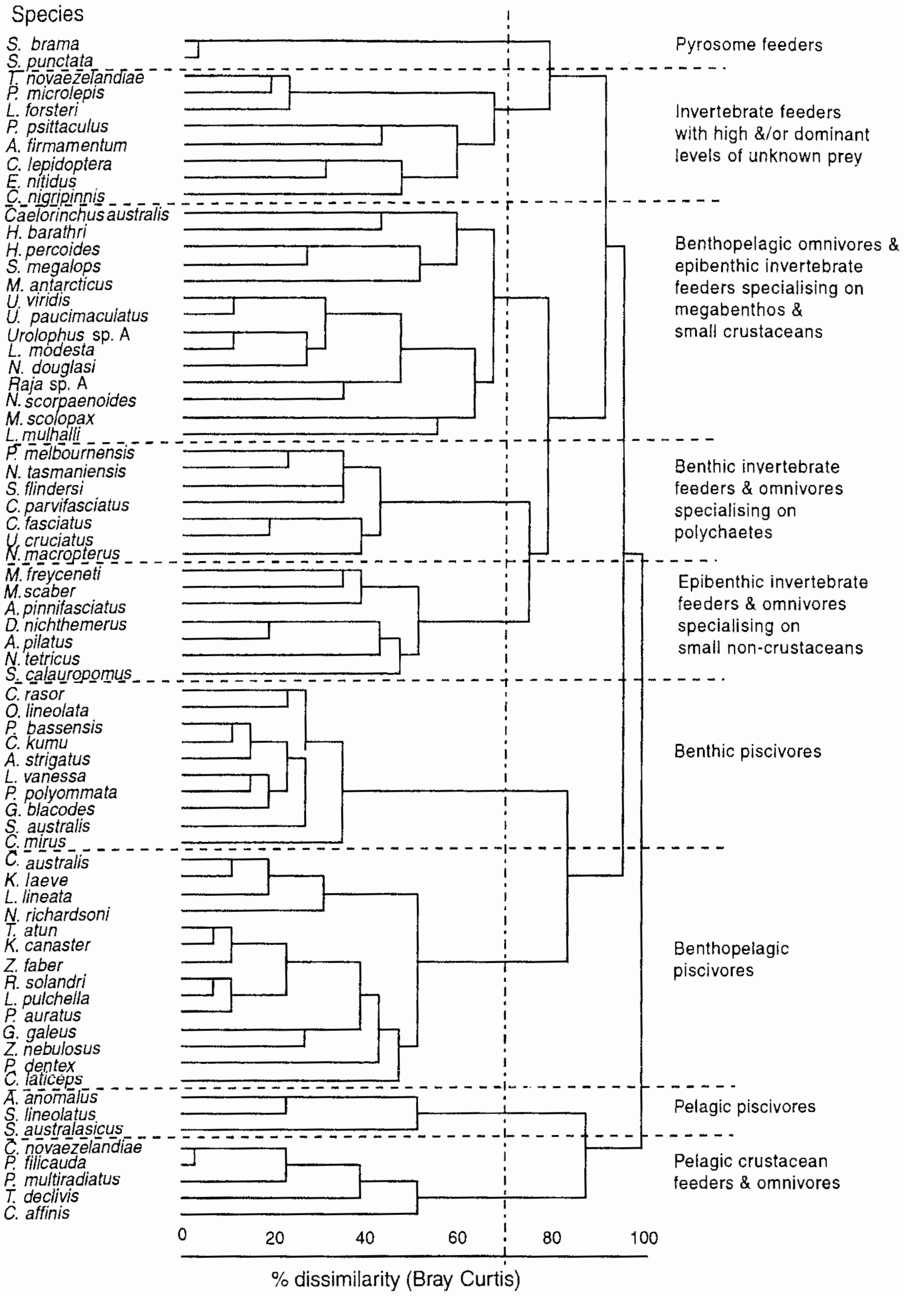


Fig. 2. Cluster dendrogram, based on Bray–Curtis dis-similarity measures of diet composition, of 70 fish species from the south-eastern Australian shelf.

species, particularly juveniles that would be more rapidly digested and unidentifiable than larger fish. It is obvious that juveniles are preyed on because we detected *N. richardsoni* feeding on *G. blacodes* that were probably the young of the year. Similarly, *Latris lineata* were probably feeding on juvenile *Helicolenus percoides*. In these cases, the relative consumption in numbers is much higher and predators could be consuming a significant proportion of the prey species' year class.

In our study, the diet of the overall community is nearly equally split between benthic and pelagic prey sources. It is expected that benthic associations are more common in fish assemblages in shallower water and that deeper species are more generalist feeders (Mauchline and Gordon 1985). Despite this, the large majority of the 12 commercial fishes in our study, relies very much on pelagic prey. Since these 12 species comprised up to 52% of the fish biomass caught in the broad scale surveys and 21% of fish caught in the

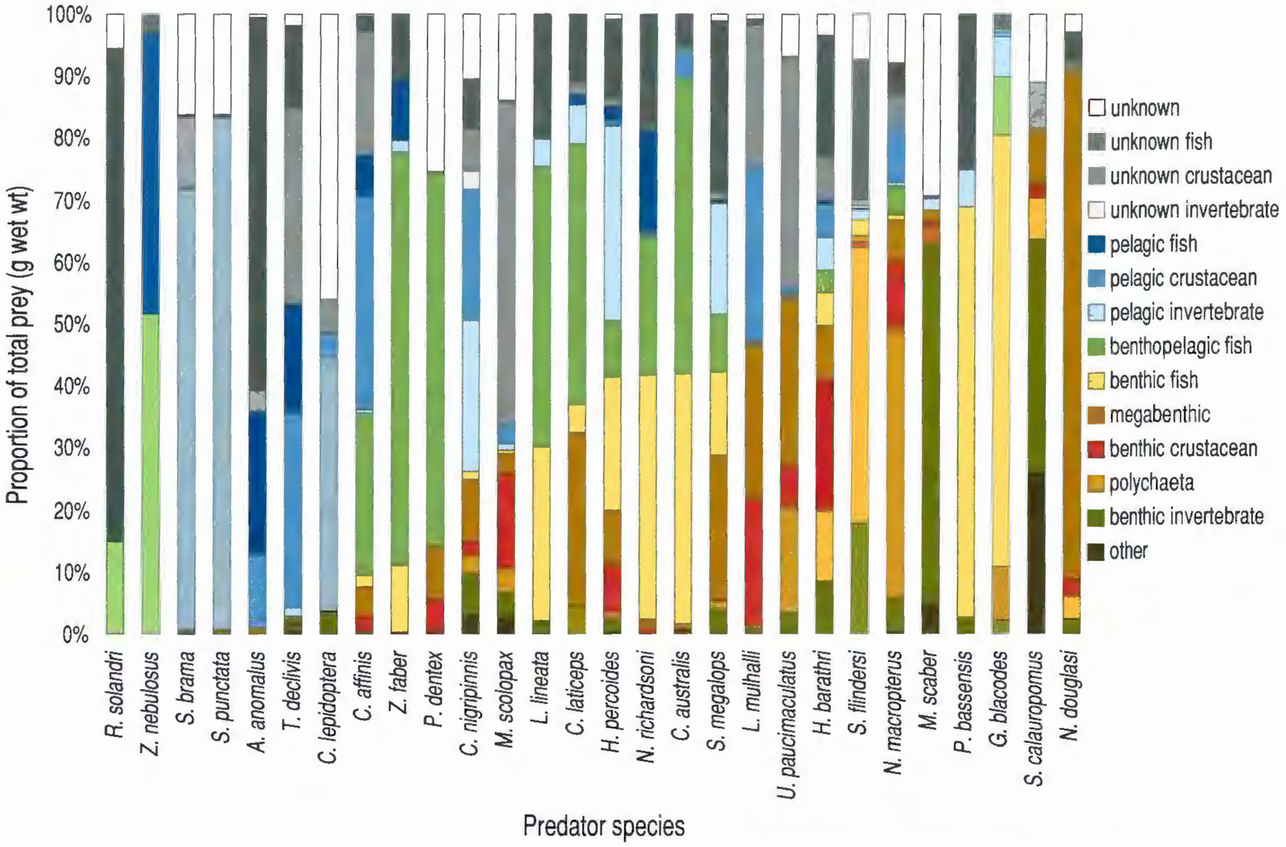


Plate I. Diet composition based on wet weight of prey for 28 fish species from the south-eastern Australian shelf. They include 12 quota species (commercial fishery) and 16 ecologically important species (see Table 2 for detailed list). Cool colours indicate pelagic prey sources and warm colours indicate benthic sources.

mesohabitats, the importance of pelagic production to the overall community becomes much more significant. Mesopelagic prey were also important to demersal fish in other coastal shelf waters (Fujita *et al.* 1995), and in deeper waters on the upper- and mid-slope (Pearcy and Ambler 1974; DuBuit 1978; Sedberry and Musik 1978; Mauchline and Gordon 1984*a*, 1984*b*, 1984*c*; Bulman and Blaber 1986; Houston and Haedrich 1986; Blaber and Bulman 1987; Gordon and Mauchline 1990). The pelagic prey of these predator species is often very abundant (Targett 1981; Bulman and Blaber 1986; Fujita *et al.* 1995) and this abundance might contribute to the reduction of competition between the predators.

The dependence on pelagic food sources, and *T. declivis*, by the species in our subset of commercially and ecologically important species, adds an interesting dimension to management of multi-species fisheries. Much of this pelagic prey was fish. Understanding the trophic structure and interactions is fundamental to understanding the dynamics of the ecosystem. Although the methodology and completeness of available information are often grossly inadequate (Pimm *et al.* 1991), food web analysis and modelling can provide better information for ecosystem management problems.

Fundamental to food-web analyses is the appropriateness of the pooling or aggregation of prey taxa. Here we used 'functional groupings' as the preferred method because we could consider size, mobility, taxa and habitat. We assumed that predators were more likely to be generalists than specialists in response to prey availability but that certain preferences such as habitat (i.e. source) or size might also be important. The resulting guilds might be too coarse and not reflect the ways in which species partition their niches. However, other factors not considered, such as depth and locality, may also be equally important. Further food web analysis may prove that these groupings need modifying.

The only previous food web structure designed for species in the same area of the SEF shelf was that of Parry *et al.* (1990). They examined trophic interactions of species from 7 to 30 m and from 30 to 50 m. Their study is based on only 12 species and a small numbers of stomach samples. Our study covers a much broader depth range, from 25 m to

Table 4. Percentage by weight of total, quota species, *T. declivis* and other fish in the fish component of the diets of 27 fish-eating species from the south-eastern Australian shelf

The quota species (indicated by *) are commercial fishery species. The 27 species are within the 28 species subset (see Table 2)

Prey type	Total fish	Quota fish	*T. declivis*	Other fish
L. lineata	93.5	17.4		76.1
**Z. faber*	97.9	11.3	43.0	43.6
**N. richardsoni*	96.4	7.8	0.7	87.9
C. laticeps	58.9	6	33.5	19.4
**C. affinis*	37.0	0.9		36.1
**N. macropterus*	10.8	0. 5		10.3
C. australis	93.3	0.4		92.9
P. bassensis	91.4	0.2		91.2
T. declivis	31.4	0.2		31.2
S. megalops	50.8	0.1		50.7
**G. blacodes*	81.3	0.1		81.2
**Z. nebulosus*	100	0	50.4	49.6
**R. solandri*	94.4	0		94.4
A. anomalus	83.1	0		83.1
**P. dentex*	60.4	0		60.4
**H. percoides*	45.6	0	4.7	40.9
**H. barathri*	28.7	0		28.7
**S. flindersi*	25.6	0		25.6
C. nigripinnis	9.2	0		9.2
N. douglasi	5.0	0		5.0
L. mulhalli	1.2	0		1.2
M. scolopax	0.6	0		0.6
U. paucimaculatus	0.2	0		0.2
C. lepidoptera	0.2	0		0.2
**S. brama*	0.2	0		0.2
**S. punctata*	0.2	0		0.2
S. calauropomus	0.1	0		0.1

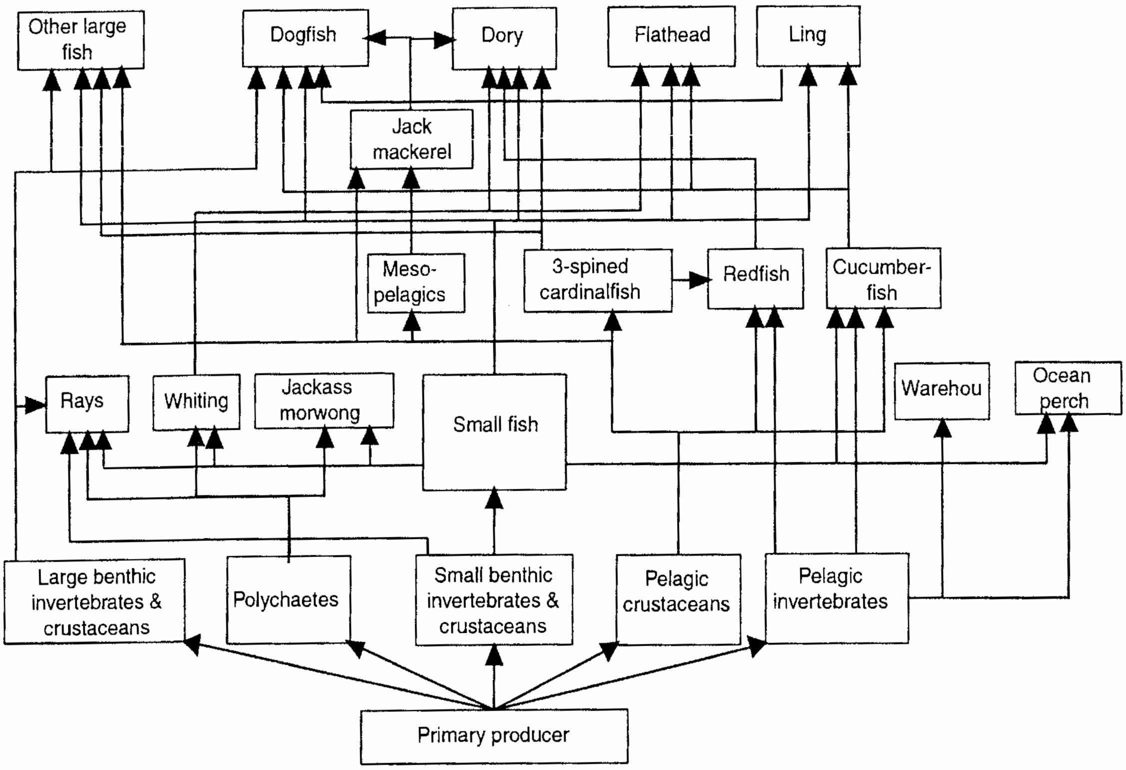


Fig. 3. Food web diagram for the south-eastern Australian shelf.

200 m, and combines all depths. We also examined a larger number of species and stomach samples. Despite this, flathead, dogfish and rays appear dominant in both studies. In our study we deliberately chose to treat certain species separately because of their importance, e.g. quota species, and so our food web was devised with further analysis of energy flows and significant interactions in mind.

In demersal ecosystems such as the SEF shelf, where prey species are diverse and their production can be driven by the outer shelf production, tightly coupled predator–prey interactions are unlikely because predators can switch to more abundant prey, or switch from pelagic to benthic prey or vice versa. We found that although there appeared to be many species of apex predators, none was abundant enough to be considered as a 'keystone' predator. Similarly, large sharks, marine mammals and birds were not considered to be keystone predators either. Such a lack of 'keystone' species is common in other marine systems (Jennings and Kaiser 1998). This suggests that the fishery may play an important role in determining fish community structure. This is commonly seen in many other marine systems (Jennings and Kaiser 1998; Hall 1999).

Acknowledgments

We are grateful to the many members of the SEF Shelf Ecosystem Project who collected samples during the field surveys on board research and commercial vessels and who assisted in the laboratory. This study was supported by the Fisheries Research and Development Corporation of Australia (FRDC project 94/040).

References

Bax, N., and Williams, A. (eds) (2000). Habitat and fisheries production in the South East Fishery ecosystem. Final Report to Fisheries Research and Development Corporation. (CSIRO: Hobart, Australia.)

Bax, N., Williams, A., Davenport, S., and Bulman, C. (1999). Managing the ecosystem by leverage points: a model for a multispecies fishery. In 'Ecosystem Approaches for Fisheries Management'. Proceedings of the 1998 Wakefield Symposium on Ecological Considerations in Fisheries Management. pp. 283–303. (Alaska Sea Grant College Program.)

Bax, N., Williams, A., and Gowlett-Homes, K. (2000). Biological communities. In 'Habitat and Fisheries Production in the South East Fishery Ecosystem'. (Eds N. Bax and A. Williams.) Final Report to Fisheries Research and Development Corporation. (CSIRO: Hobart, Australia.)

Blaber, S. J. M. and Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345–56.

Bulman, C. M., and Blaber, S. J. M. (1986). Feeding ecology of *Macruronus novaezelandiae* (Hector)(Teleostei: Merluciidae) in south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **37**, 621–39.

DuBuit, M. H. (1978). Alimentation de quelques poissons téléostéens de profondeur dans la zone du seuil de Wyville Thomson. *Oceanologica Acta* **1**, 129–34.

Fujita, T., Kitagawa, D., Okuyama, Y., Ishito, Y., Inada, T. and Jin, Y (1995). Diets of the demersal fishes on the shelf off Iwate, northern Japan. *Marine Biology* **123**, 219–33.

Gomon, M. F., Glover, J. C. M., and Kuiter, R. H. (eds)(1994). 'The Fishes of Australia's South Coast.' (State Print: Adelaide, Australia.) 992 pp.

Gordon, J. D. M., and Mauchline, J. (1990). Depth-related trends in diets of a seep-sea bottom-living fish assemblage of the Rockall Trough. In 'Trophic Relationships in the Marine Environment'. Proceedings of the 24th European Marine Biology Symposium. (Eds M. Barnes and R. N. Gibson.) pp. 439–52. (Aberdeen University Press: Aberdeen.)

Hall, S. J. (1999). 'The Effects of Fishing on Marine Ecosystems and Communities.' (Blackwell Science: London.) p. 274.

Houston, K. A., and Haedrich, R. L. (1986). Food habits and intestinal parasites of deep demersal fishes from the upper continental slope east of Newfoundland, northwest Atlantic Ocean. *Marine Biology* **92**, 563–74.

Jaksic, F. M., and Medel, R. G. (1990). Objective recognition of guilds: testing for statistically significant species clusters. *Oecologia* **82**, 87–92.

Jennings, S., and Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. In 'Advances in Marine Biology'. (Eds J. H. S. Baxter, A. H. Southward and P. A. Tyler.) pp. 203–343. (Academic Press: London.)

Jones, D. S. and Morgan, G. J. (1994). 'A Field Guide to Crustaceans of Australian Waters.' (Reed: Sydney, Australia.) 216 pp.

Last, P. R., Scott, E. O. G., and Talbot, F. H. (1983). 'Fishes of Tasmania.' (Tasmanian Fisheries Development Authority: Hobart, Australia.) 563 pp.

Mauchline, J., and Gordon, J. D. M. (1984*a*). Feeding and bathymetric distribution of the gadoid and morid fish of the Rockall Trough. *Journal of the Marine Biological Association U. K.* **64**, 657–65.

Mauchline, J., and Gordon, J. D. M. (1984*b*). Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. *Journal du Conseil International pour l'Exploration de la Mer* **41**, 239–47.

Mauchline, J., and Gordon, J. D. M. (1984*c*). Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean. *Marine Biology* **81**, 107–21.

Mauchline, J. and Gordon, J. D. M. (1985). Trophic diversity in deep-sea fish. *Journal of Fish Biology* **26**, 527–35.

Parry, G. D., Campbell, S. J., and Hobday, D. K. (1990). Marine resources off east Gippsland, southeastern Australia. Marine Science Laboratories Technical Report No. 72. 166 pp.

Pearcy, W. G., and Ambler, J. W. (1974). Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep Sea Research* **21**, 745–59.

Pimm, S. L., Lawton, J. H., and Cohen, J. E. (1991). Food web patterns and their consequences. *Nature* **350**, 669–74.

Sedberry, G. A., and Musick, J. A. (1978). Feeding strategies of some demersal fishes of the continental slope and rise off the mid-Atlantic coast of the USA. *Marine Biology* **44**, 357–75.

Targett, T. E. (1981). Trophic ecology and structure of coastal Antarctic fish communities. *Marine Ecology Progress Series* **4**, 243–63.

Tilzey, R. D. J. (1994). Introduction. In 'The South East Fishery'. (Ed. R. D. J. Tilzey.) pp. 15–40. (Bureau of Resource Sciences: Canberra, Australia.) 360 pp.

Tilzey, R. D. J. (ed.) (1999). 'The South East Fishery 1998, Fishery Assessment Report Compiled by the South East Fishery Assessment Group.' (Australian Fisheries Management Authority: Canberra, Australia.) 199 pp.

Williams, A., and Bax, N. J. (2001). Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52**, 513–36.

Williams, H., and Pullen, G. (1993). Schooling behaviour of jack mackerel *Trachurus declivis* (Jenyns) observed in the Tasmanian Purse-seine fishery. *Australian Journal of Marine and Freshwater Research* **44**, 577–87.

Young, J. W., Jordan, A. R., Bobbi, C., Johannes, R. E., Haskard, K., and Pullen, G. (1993). Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern Tasmania, Australia. *Marine Biology* **116**, 9–18.

Manuscript received 3 November 1999; revised and accepted 28 February 2000

Mar. Freshwater Res., 2001, **52**, 549–61

Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing

K. J. Graham, N. L. Andrew[A] *and K. E. Hodgson*[B]

NSW Fisheries Centre, PO Box 21, Cronulla, NSW 2230, Australia
[A]Present address: National Institute of Water and Atmospheric Research, PO Box 14-901 Kilbirnie, Wellington, New Zealand
[B]Present address: Tasmanian Aquaculture & Fisheries Institute, Nubeena Crescent, Taroona, Tas. 7053, Australia

Abstract. Upper continental slope trawling grounds (200–650 m depth) off New South Wales were surveyed with the same vessel and trawl gear and similar sampling protocols in 1976–77 (during the early years of commercial exploitation) and in 1996–97. The 1996–97 mean catch rate of sharks and rays, pooled for the main 15 species (or species groups), was ~20% of the 1976–77 mean. Individual catch rates were substantially lower in 1996–97 for 13 of the 15 species or species groups. The greatest decline was observed for dogsharks of the genus *Centrophorus*, which were most abundant in 1976–77 but rarely caught 20 years later. In contrast, 1996–97 catch rates of spiky dogshark (*Squalus megalops*) and, to a lesser extent, whitefin swell shark (*Cephaloscyllium* sp. A) were similar to those in 1976–77. Trawling during 1979–81 provided data for nine species, albeit not corrected for larger gear size, and the pooled mean catch rate for sharks and rays in the depth range 300–525 m was ~28% of the mean for 1976–77. The results suggest that the biomass of most species of sharks and rays declined rapidly as the fishery developed and is now at very low levels.

Introduction

The difficulties of sustainably harvesting sharks and rays, and the consequent failures of management, have been highlighted by many authors (e.g. Holden 1974; Anderson 1990; Hoenig and Gruber 1990; Pratt and Casey 1990; Shotton 1999; Walker 1999). This problem is particularly acute in multi-species trawl fisheries in which sharks and rays are only a relatively minor bycatch (Compagno 1990); such fisheries often continue long after the collapse of the cartilaginous fish stocks. The probability of sustainable exploitation is further diminished by poor knowledge of the biology and ecology of many sharks and rays, particularly deepwater species.

The demersal trawl-fishery on the continental slope around south-eastern Australia shares many of the above impediments to sustainable exploitation of sharks. Off New South Wales (NSW), commercial trawling on the upper slope began in 1968. Two vessels operating out of Wollongong targeted mainly redfish (*Centroberyx affinis*) but also landed substantial quantities of gemfish (*Rexea solandri*), mirror dory (*Zenopsis nebulosus*) and edible shark (Diorio 1976). By 1974, there were about 12 vessels trawling the slope off Wollongong and Sydney but the main expansion of the fishery was between 1975 and 1980 following exploratory trawling by the NSW Government's fisheries research vessel *Kapala* (Crozier and Graham 1978; Graham and Gorman 1985). By the early 1980s, more than 100 trawlers between 15 and 25 m in length operated off NSW and landed about 15 000 t of fish per year; about 60 of these trawlers regularly fished on the upper slope (Graham *et al.* 1982).

Between 1977 and 1988, catches from the upper slope accounted for more than half of the trawl-fish landings in NSW. The majority of the catch consisted of gemfish, redfish, mirror dory, ling (*Genypterus blacodes*) and ocean perch (*Helicolenus barathri*). Significant landings of edible shark, principally dogsharks (fam. Squalidae) and angel shark (*Squatina* sp.), were also made but detailed catch statistics were not recorded for these species. It is likely, however, that during the early years, substantial quantities of dogsharks were discarded by trawlers in preference to the more marketable teleosts. By the late 1980s, catch rates of several upper slope species off NSW, in particular gemfish and redfish, had declined markedly (Rowling 1994*a*, 1994*b*, 1997). In 1992, management controls in the form of Total Allowable Catches and Individual Transferable Quotas for 15 species of teleosts were introduced into what became the South East Fishery (SEF), including NSW (Tilzey 1994). By the end of the 1990s, the number of trawlers regularly fishing the NSW slope grounds was about 40.

The fact that no management controls were applied to any species of shark or ray almost certainly reflected their low level of abundance and economic importance at the

10.1071/MF99174 1323-1650/01/040549

time controls for teleosts were introduced. Although sharks were never a major part of the landed catch in the SE trawl fishery, angel shark, gummy shark (*Mustelus antarcticus*), sawshark (*Pristiophorus* spp.) and the larger species of dogsharks were a valuable bycatch. In recent years a market for squalene, an oil extracted from the livers of many deepwater dogsharks, has added to the value of those sharks. However, landings of upper slope sharks by NSW trawlers are now at very low levels (Liggins 1997).

In 1976–77 and 1996–97, stratified surveys by FRV *Kapala* were done on trawl grounds off central and southern NSW in depths between 200 and 650 m. Surveys were also done over a depth range of 300–525 m on the same grounds in 1979–81. Details of the 1996–97 survey were presented in Graham *et al.* (1997) and a more comprehensive analysis of the differences among surveys and depths between the 1976–77 and 1996–97 periods was reported for important teleosts and elasmobranchs by Andrew *et al.* (1997). In this paper, we document the relative abundances of 15 species (or species groups) of sharks (including ghostshark) and rays on the NSW upper slope from the three survey periods between 1976 and 1997. Because the initial survey was done close to the beginning of the fishery, the results provide a rare opportunity to describe any changes in relative abundance after 20 years of trawling on previously unexploited stocks.

Materials and methods

Upper slope trawling grounds (depth range 200–650 m) were surveyed off Sydney–Newcastle, Ulladulla–Batemans Bay and Eden–Gabo Island (referred to below as Sydney, Ulladulla and Eden; Fig. 1). These grounds were described in detail by Graham and Gorman (1985). The upper slope between Newcastle and the 'Horseshoe' (a canyon and rough seabed area indenting the continental shelf south-west of Gabo Island) is narrow (3–5 nmile wide) with an overall area of about 1290 sq. nmile, ~ 75% of which is trawlable. The area of the three survey grounds was about 440 sq. nmile of which 65% was surveyed.

The three grounds were surveyed in 1976–77 and again in 1996–97 using the same vessel and trawl gear of the same design and dimensions. The headline length of the trawl nets was 21 m, and the total length of the sweep and bridles on each side was 75 m (see Graham *et al.* 1997 for gear details). The Sydney and Ulladulla grounds were surveyed twice in each of 1976, 1977 and 1996; the Eden area was surveyed three times in 1977, twice in 1996 and once in 1997. The 1996–97 surveys were done at the same time of the year as those in 1976–77. At each location, tows (usually three) were done along each of eight isobaths: 220, 275, 330, 385, 440, 495, 550 and 605 m. Logistic constraints reduced the number of tows per isobath during some surveys. Trawling speed was approximately 3.0 kn. In both the 1976–77 and 1996–97 survey periods, data from tows in adjacent depths were pooled into four depth zones. These depth zones were: 1, 220–275 m; 2, 330–385 m; 3, 440–495 m; and 4, 550–605 m.

During 1976–77, the order of depths was randomized but on most occasions, two or three of the tows within a particular depth were done on the same day. Tow duration was initially 2 h (Sydney, Survey 1) but thereafter mostly for 1 h; of the 246 tows done in 1976–77, 219 were for 1 h. Most (85%) tows were done in daylight; night-time tows were in the evening, soon after nightfall. In 1996–97, all 159 tows were for 1 h at 3.0 kn during daylight. The random order in which tows were done was constrained such that only one tow was done per isobath per day and, unless unavoidable, adjacent depths were not sampled within any day.

Supplementary data were derived from surveys and other trawling done between 1979 and 1981 on the same grounds as the 1976–77 surveys. A range of net designs, sizes and trawl configurations was used in these surveys (Andrew *et al.* 1997). In all instances the trawls were the same size or larger than those used in 1976–77 and we assume that the fishing power of the trawls used in 1979–81 was equal to or greater than that of the standard nets used in 1976–77 and 1996–97. No attempt was made to standardize catch rates for the 1979–81 nets. Because the main target species was gemfish, most tows were done during June–October and in depths between 300 and 500 m. Consecutive tows were seldom in the same depth, and the same depth was only occasionally sampled twice per day. Tow duration was between 30 and 120 min, with 70% of tows for 60 min; 95% of tows were during daylight. Sampling protocols were otherwise the same as those described for the 1976–77 surveys.

Because of differences in the nature and structure of the 1979–81 survey design, comparisons with the other surveys were possible only for data from tows in depths equivalent to Zones 2 and 3 (see above). Data for species normally caught in Depth Zones 2 and 3 (based on

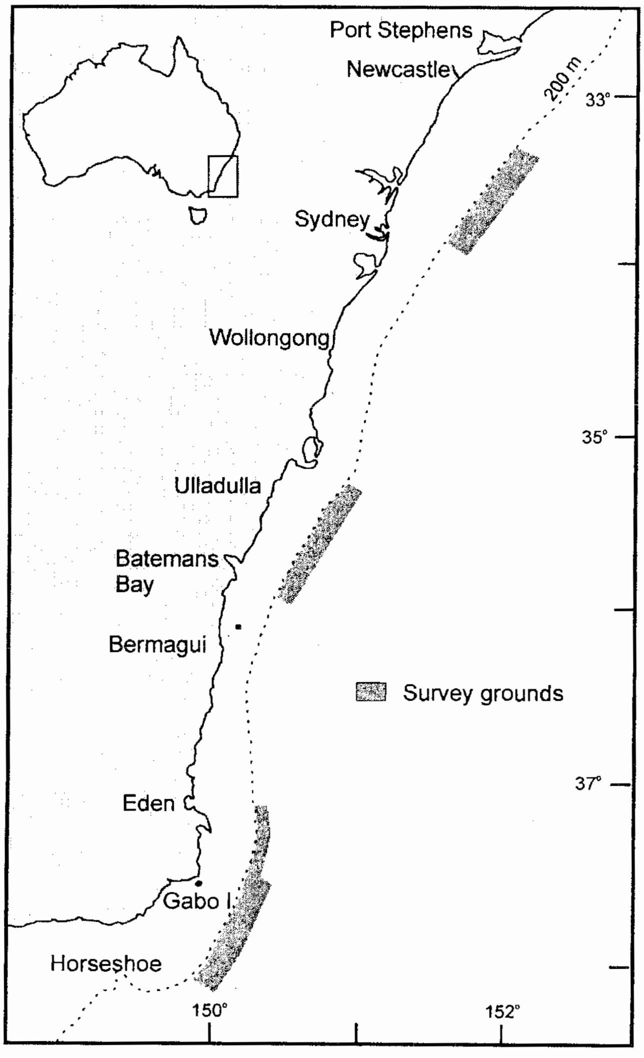


Fig. 1. Map of the NSW coast showing locations of survey grounds.

1976–77 data) were pooled for tows between 300 and 525 m at each location. For the purposes of comparisons, data from 1976–77 and 1996–97 tows in Depth Zones 2 and 3 (or only Zone 2 for the shallower water species) were aggregated in the same manner and presented as mean catch rates for each survey period.

During all surveys, total weights of each species (or species group) were recorded for each tow. Where necessary, tows were standardized to 1 h by simple proportional scaling. All catch rates are presented as pooled means (± 1 s.e.) either in the text or in tables. Mean catch rates (± 1 s.e.) are presented at the lowest level (i.e. for each survey, depth and location) for the 10 most important species or species groups as figures (Figs 2–11). Lengths (by sex) of commercially important species of sharks were collected from most catches in 1976–77 and all catches in 1996–97. Large catches were randomly subsampled for length data.

Taxonomic nomenclature follows Last and Stevens (1994). For uniformity, the common name 'dogshark' has been preferred for all species in the family Squalidae. In general, the term 'sharks and rays' refers to all chondrichthyans, including ghostsharks (chimaeras).

Results

1976–77 and 1996–97 surveys

In total, 51 species of chondrichthyans were identified in the catches in 1976–77 (43 spp.) and 1996–97 (46 spp.). Detailed catch data are presented for 15 species or species combinations of commercially important or commonly caught non-commercial sharks and rays. Length data were collected for most sharks but there was either no detectable difference between the 1976–77 and 1996–97 data (e.g. spiky dogshark) or, as for most species, there were too few caught in 1996–97 to meaningfully compare with the early data (Andrew *et al.* 1997).

A total of 246 tows was completed in 1976–77 (Sydney 93 tows, Ulladulla 90 and Eden 63) and 159 tows in 1996–97 (Sydney 48, Ulladulla 48 and Eden 63). Across all grounds, surveys and depths, a total of 167 t of fish (teleosts, sharks and rays) was caught in 1976–77 at a mean catch rate of 681 kg h^{-1}. In 1996–97 the total catch was 36 t and the mean catch rate was 216 kg h^{-1}, representing a 68% reduction in overall catch rate (Table 1).

The shark and ray component of the total catch (across all grounds) was 79.6 t in 1976–77 and 10.6 t in 1996–97. The 1996–97 mean catch rate of 65 kg h^{-1} was approximately 20% of the 323 kg h^{-1} recorded in 1976–77 (Table 1). Off Sydney, the overall shark and ray catch rate in 1996 (131 kg h^{-1}) was about 40% of that in 1976–77 and was dominated by spiky dogshark. When the spiky dogshark data are excluded, the 1996 mean catch rate for Sydney was less than 10% of the initial level. On both the Ulladulla and Eden grounds, the 1996–97 mean catch rates were about 10% of those in 1976–77. Within depth zones, mean catch rates of similar magnitude for both survey periods were recorded only off Sydney in Depth Zones 1 and 2, and in Zone 1 off Ulladulla and Eden (Fig. 2). In those depths, the relatively large catches of spiky dogshark taken during both 1976–77 and 1996–97 were a major proportion of the overall catches (see below).

The 15 sharks and rays to be discussed can be divided into two groups according to their capture depths. The first consists of species caught across most or all survey grounds and depth zones. It includes Harrissons dogshark (*Centrophorus harrissoni*), southern dogshark (*C. uyato*), Endeavour dogshark (*C. moluccensis*), greeneye dogsharks (*Squalus* spp.), longsnout dogshark (*Deania quadrispinosa*), whitefin swell shark (*Cephaloscyllium* sp. A), sharpnose sevengill shark (*Heptranchias perlo*), silver ghost shark (*Hydrolagus ogilbyi*) and skates (*Raja* spp.). The second group, comprising spiky dogshark, eastern angel shark (*Squatina* sp. A), gummy shark, eastern sawshark (*Pristiophorus* sp. A), school shark (*Galeorhinus galeus*) and stingarees (*Urolophus* spp.), were species caught mainly in Depth Zones 1 and 2; species in this group also inhabit mid- to outer-shelf depths (100–200 m) as well as the shallow upper slope depths.

Harrissons and southern dogsharks were not separated in the two 1976 surveys off Sydney, and the initial 1976 survey off Ulladulla. In those 1976–77 surveys when the two species were separated, southern dogshark formed approximately 75% of the combined catch (Table 1). To compare catch rates across all grounds and surveys, data for the two species were combined. Harrissons and southern dogsharks were caught in all depths on all grounds and they represented about 9%, 18% and 32% of the 1976–77 total fish catches off Sydney, Ulladulla and Eden, respectively (Table 1). The greatest catches were in Depth Zones 3 and 4 off Ulladulla and Eden (Fig. 3). Mean catch rates varied greatly within surveys and depths with individual catches as high as 1600 kg off Ulladulla and 2700 kg on the Eden ground. In 1976–77, the overall mean catch rate (for data pooled across all grounds and depths) was 126 kg h^{-1}. In contrast, a total of only 14 southern and 8 Harrissons dogsharks (total catch of 67 kg, mean catch rate 0.4 kg h^{-1}) was caught in 1996–97. This formed less than 1% of the total catch weight of fish caught on the three grounds.

Endeavour dogsharks were caught in all depths off Sydney (mean 25 kg h^{-1}) and Ulladulla (mean 8 kg h^{-1}) in 1976–77, but only two individuals were caught off Eden (Table 1). Mean catch rates on the Ulladulla ground were relatively high during the first survey in 1976 (max. 71 kg h^{-1} in Zone 3) but consistently low (<5 kg h^{-1}) across all depths during later surveys (Fig. 4). In 1996–97, only 12 Endeavour dogsharks (24 kg) were caught off Sydney (mean catch rate 0.5 kg h^{-1}) and none was caught off Ulladulla or Eden.

The 1976–77 greeneye dogshark catches are now believed to have included two species (*Squalus* sp. F and *S. mitsukurii*). The bi-modal nature of the length–frequency data for males (Andrew *et al.* 1997) suggests that the two species were caught in approximately equal numbers off Sydney and Ulladulla, whereas the Eden data indicate that 75% or more of the greeneye dogshark catch in the southern

Table 1. **Mean catch rates (kg h^{-1} and 1 s.e.) for total fish, total sharks and rays, and main species caught during 1976–77 and 1996–97**

For comparison, data were pooled across all depth strata (220–605 m). For those species caught almost exclusively in the shallower depths, data were pooled across Zones 1 and 2

	1976–77								1996–97							
	All Areas		Sydney		Ulladulla		Eden		All Areas		Sydney		Ulladulla		Eden	
	Mean catch (kg h^{-1})	s.e.	Mean catch (kg h^{-1})	s.e.	Mean catch (kg h^{-1})	s.e.	Mean catch (kg h^{-1})	s.e.	Mean catch (kg h^{-1})	s.e.	Mean catch (kg h^{-1})	s.e.	Mean catch (kg h^{-1})	s.e.	Mean catch (kg h^{-1})	s.e.
Depth Zones 1–4 (220–605 m)																
No. of tows	246		93		90		63		159		48		48		63	
Total fish	680.9	49.0	548.2	36.7	847.7	117.1	638.6	70.6	215.7	18.3	222.2	45.3	166.4	14.7	253.0	30.2
Total sharks & rays	322.9	21.5	317.8	28.2	311.4	35.1	346.9	53.7	65.1	13.7	130.5	43.5	33.1	6.1	39.7	5.6
Harrissons & southern dogsharks	126.3	17.7	49.5	9.1	151.8	31.6	203.4	48.3	0.4	0.1	0.2	0.2	1.0	0.4	<0.1	
Harrissons dogshark[A]	28.8	4.2	14.6	3.0	24.3	5.2	43.6	9.6	0.1	0.1	0.2	0.2	0.1	0.1	0	
Southern dogshark[A]	106.9	21.0	27.1	6.1	106.2	30.4	163.4	46.7	0.3	0.1	0		0.9	0.4	0.3	0.3
Greeneye dogsharks	44.8	5.5	92.4	12.7	21.8	3.1	7.5	2.2	1.2	0.3	2.7	0.7	1.2	0.6	<0.1	
Skates	32.7	3.0	33.0	4.3	32.6	6.1	32.4	4.5	5.5	0.8	8.1	1.9	3.9	0.9	5.0	1.2
Endeavour dogshark	12.3	1.8	24.5	3.9	8.1	2.4	0.1	0.1	0.2	0.1	0.5	0.2	0		0	
Longsnout dogshark	11.0	1.8	9.4	2.8	12.4	2.8	11.4	3.9	1.4	0.4	0.2	0.2	2.7	1.0	1.2	0.6
Silver ghostshark	8.3	1.2	7.9	1.7	2.2	0.6	17.4	3.3	0.3	0.1	0.6	0.2	0.3	0.1	<0.1	
Whitefin swell shark	7.2	0.8	2.8	0.5	6.0	0.8	15.7	2.7	4.9	0.9	1.2	0.3	3.6	1.2	8.9	2.1
Sharpnose 7gill shark	3.5	0.7	6.9	2.0	1.8	0.5	1.2	0.3	0.3	0.1	1.0	0.3	<0.1		0	
Depth Zones 1–2 (220–385 m)																
No. of tows	132		49		48		35		83		24		24		35	
Total fish	700.7	77.4	675.4	55.3	920.7	198.0	430.2	70.6	246.0	31.6	378.2	78.6	131.1	11.3	247.2	52.5
Total shark & ray	299.3	22.1	416.4	44.3	230.5	25.0	229.6	34.6	108.2	25.4	249.2	81.5	46.1	11.4	54.2	8.6
Spiky dogshark	64.0	7.4	82.2	14.5	61.8	11.3	41.5	10.6	75.5	22.3	192.4	74.7	28.4	8.4	31.7	7.8
Eastern angel shark	32.6	5.3	27.3	6.3	60.8	11.9	1.5	0.6	1.3	0.4	2.7	0.8	1.2	0.7	0.4	0.4
Stingarees	19.5	4.1	38.2	10.3	8.5	2.9	9.5	2.5	6.7	2.0	21.0	6.4	1.6	0.8	0.9	0.3
Gummy shark	5.5	1.1	4.1	1.3	2.6	0.7	11.3	3.3	1.1	0.3	2.7	0.9	<0.1		0.7	0.4
Eastern sawshark	4.8	0.9	8.5	2.0	2.0	0.5	3.4	1.4	2.5	0.8	7.9	2.4	0.3	0.1	<0.1	
School shark	3.4	1.0	0.1	0.1	5.6	2.5	4.9	1.8	0		0		0		0	

[A] Data from tows when species was recorded separately.

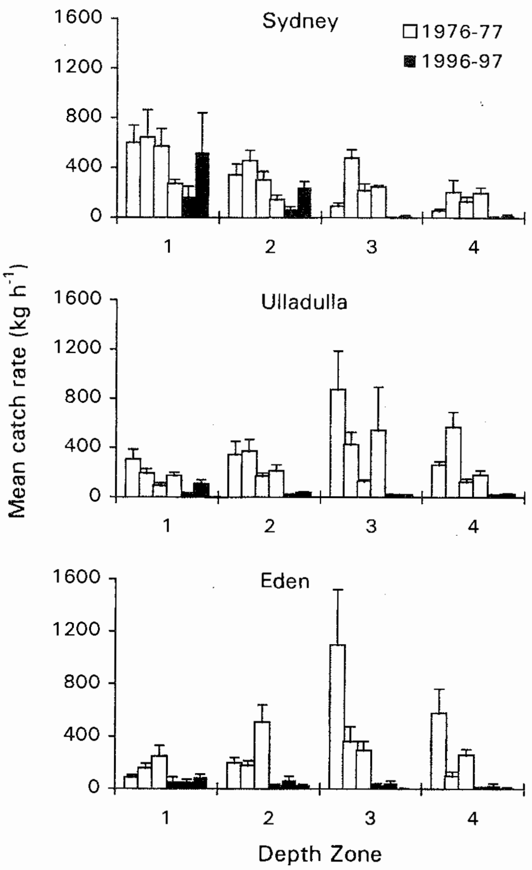


Fig. 2. Mean catch rates (kg h^{-1} + 1 s.e.) for total sharks and rays at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

area comprised *S. mitsukurii.* The 1976–77 catch rates of greeneye dogsharks were greatest off Sydney (mean 92 kg h^{-1}), and were progressively lower off Ulladulla (22 kg h^{-1}) and Eden (8 kg h^{-1}) (Table 1). On the Sydney ground, catch rates generally decreased with increasing depth (Fig. 5). In 1996–97, the mean catch rate was 3 kg h^{-1} off Sydney and 1 kg h^{-1} off Ulladulla; the catches included both species but over 80% (by number) were *Squalus* sp. F. Off Eden, a single *S. mitsukurii* was caught in 1997.

Longsnout dogshark catches were greatest in Depth Zones 3 and 4 off Sydney and in Zone 4 on the Ulladulla and Eden grounds, although catch rates were highly variable among surveys (Fig. 6). When the data were pooled across depths, the 1976–77 mean catch rates were similar for all grounds and the overall catch rate (11.0 kg h^{-1}) was substantially higher than the 1.4 kg h^{-1} recorded in 1996–97. The 1996–97 catches of longsnout dogshark were almost totally confined to Zone 4 off Ulladulla and Eden (Table 1, Fig. 6).

The whitefin swell shark was caught in all depths on all grounds and overall catch rates were similar during both survey periods (Fig. 7). Across all grounds and depths, the mean catch rate of 4.9 kg h^{-1} in 1996–97 was 68% of the

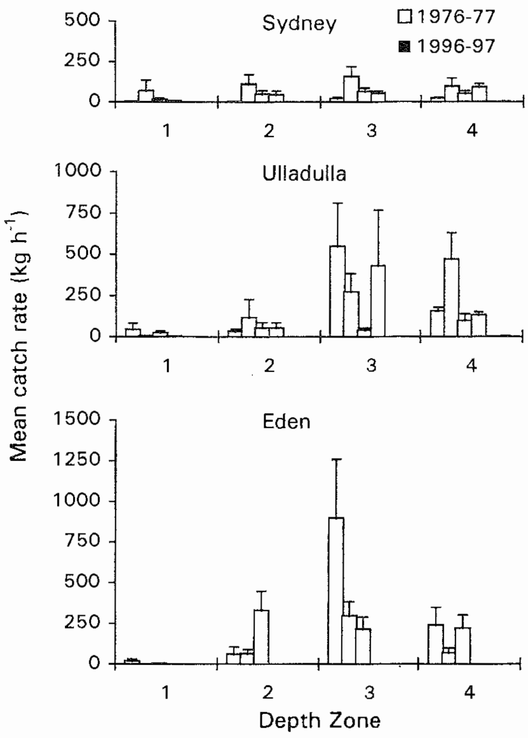


Fig. 3. Mean catch rates (kg h^{-1} + 1 s.e.) for Harrissons (*Centrophorus harrissoni*) and southern (*C. uyato*) dogsharks (combined) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

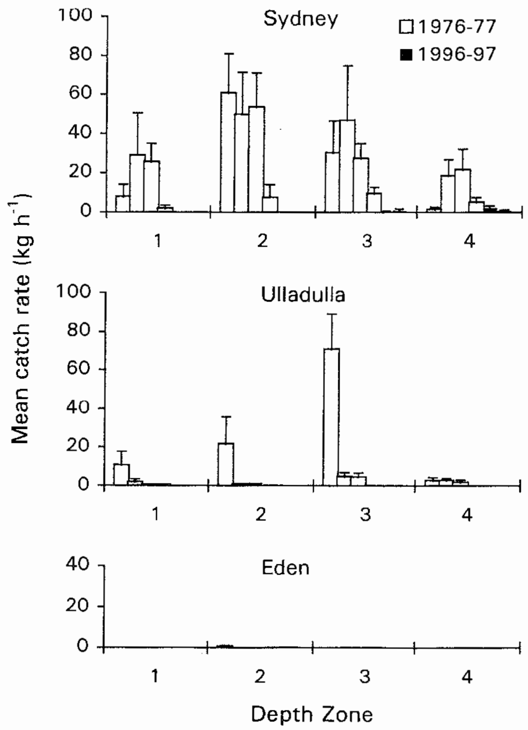


Fig. 4. Mean catch rates (kg h^{-1} + 1 s.e.) for Endeavour dogshark (*Centrophorus moluccensis*) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

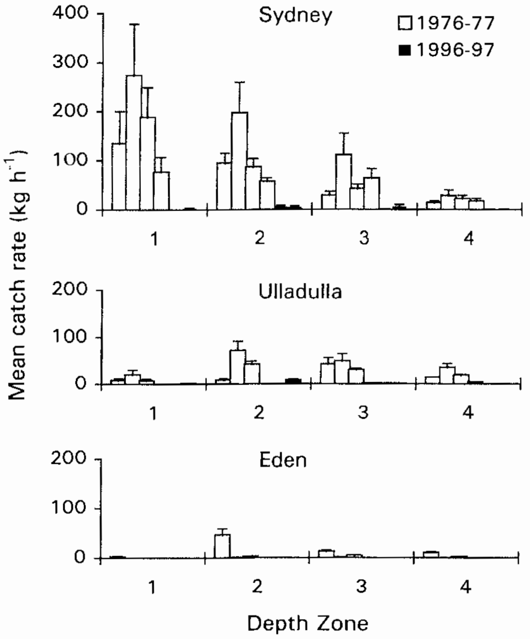


Fig. 5. Mean catch rates (kg h^{-1} + 1 s.e.) for greeneye dogsharks (*Squalus* sp. F & *S. mitsukurii*) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

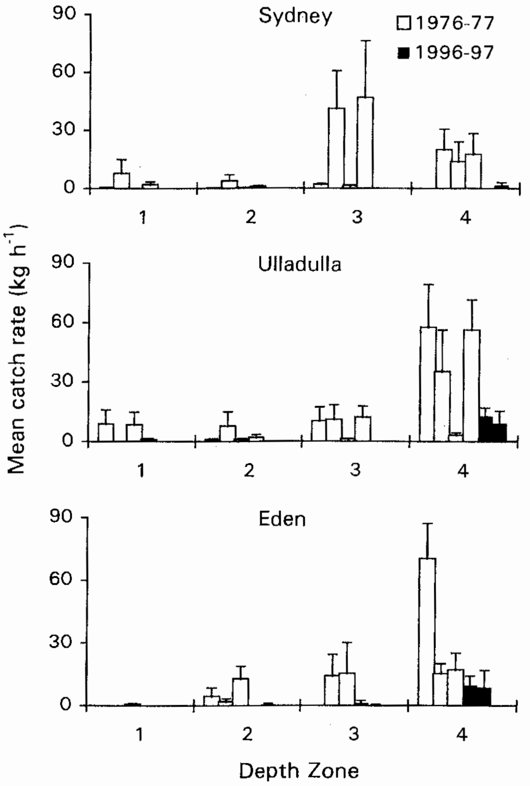


Fig. 6. Mean catch rates (kg h^{-1} + 1 s.e.) for longsnout dogshark (*Deania quadrispinosa*) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

1976–77 mean (7.2 kg h^{-1}) (Table 1). This species was most abundant off Eden during both survey periods (15.7 and 8.9 kg h^{-1}).

Eight species of skates in the genus *Raja* were recorded during the surveys. Two species (*Raja* sp. B and *R. gudgeri*) dominated catches of skate in Depth Zones 2–4 on all grounds. Zone 1 catches mainly comprised *Raja australis*, but off Sydney also included *Raja* sp. C, and off Ulladulla and Eden, *Raja* sp. A and *R. whitleyi*. *Raja* sp. C was also common in Zones 2 and 3 off Sydney; small numbers of *Raja* sp. I and *Raja* sp. J were present in Zone 4 catches on all grounds. Catch data were pooled for all species. In 1976–77, mean catch rates for skates were similar on all grounds (range 32–33 kg h^{-1}) but were substantially lower in 1996–97 (range 4–8 kg h^{-1}) (Table 1). Catches were greatest in Zone 3 on all grounds (Fig. 8).

Silver ghostsharks were identified as *Hydrolagus ogilbyi* but a similar second species (*H. lemures*) reported from off NSW (Last and Stevens 1994) also may have been caught. Catches of silver ghostshark were greatest in Zones 1 and 2 off Sydney and Zones 2 and 3 off Eden, although variable among surveys within zones (Fig. 9). Several catches off Sydney and Eden exceeded 50 kg h^{-1} (maximum 110 kg h^{-1}) in a number of depths; the greatest catch in any tow during 1996–97 was 7 kg. The pooled mean catch rate for silver ghostsharks in 1976–77 was 8.3 kg h^{-1} but in 1996–97 was less than 1 kg h^{-1} (Table 1).

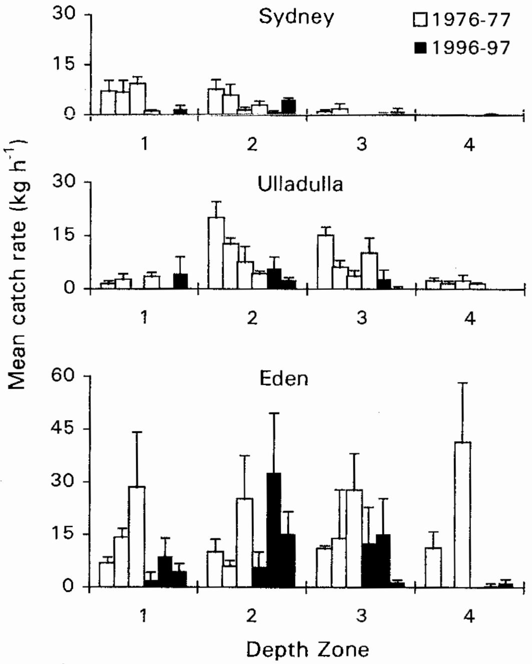


Fig. 7. Mean catch rates (kg h^{-1} + 1 s.e.) for whitefin swell shark (*Cephaloscyllium* sp. A) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

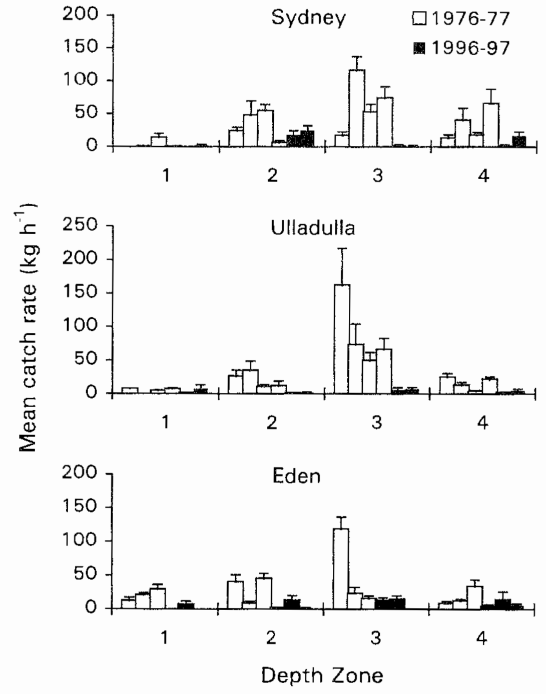


Fig. 8. Mean catch rates (kg h^{-1} + 1 s.e.) for skates (*Raja* spp.) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

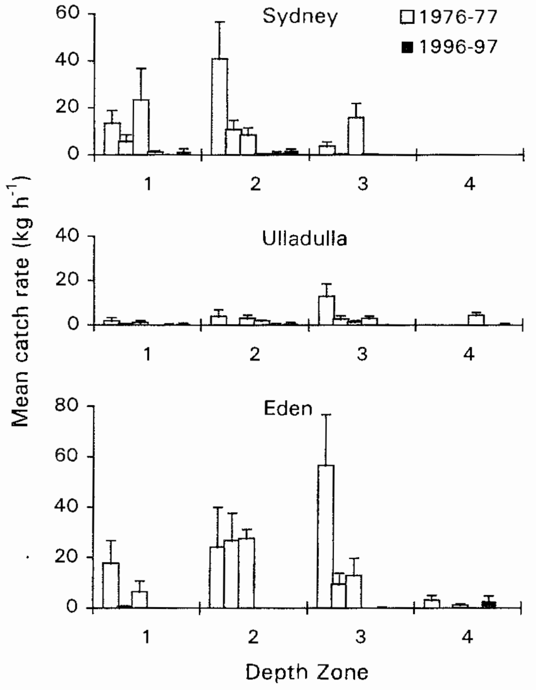


Fig. 9. Mean catch rates (kg h^{-1} + 1 s.e.) for silver ghostshark (*Hydrolagus ogilbyi*) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

Small quantities of sharpnose sevengill shark were caught on all grounds. Catch rates were greatest off Sydney, particularly in Zones 1 and 2. The overall mean catch off Sydney in 1976–77 was 6.9 kg h^{-1} but only 1.0 kg h^{-1} in 1996 (Table 1). Off Ulladulla and Eden, the 1976–77 mean catch rates were relatively low (1.8 and 1.2 kg h^{-1}, respectively), but in 1996–97 only a single sharpnose sevengill shark was caught off Ulladulla and none off Eden.

Of the species caught principally in Depth Zones 1 and 2, spiky dogshark was the most abundant. Spiky dogshark was caught only in Depth Zones 1 and 2 off Sydney and Ulladulla, but in 1996 a small catch (12.5 kg) was also taken in Depth Zone 3 off Eden (Fig. 10). When data were pooled across surveys and depths, the 1996–97 mean catch rate off Sydney was higher than in 1976–77, but with significant variability around the estimates (Fig. 10). The Sydney catch rate in 1996 included a single catch of 1800 kg h^{-1} boosting the mean to 192 kg h^{-1}, more than double the 1976–77 mean of 82 kg h^{-1} (Table 1). On the two southern grounds, the 1976–77 mean catch rates were 62 and 42 kg h^{-1} for Ulladulla and Eden, respectively, compared with 28 and 32 kg h^{-1} in 1996–97 (Table 1). For each of the grounds, the size composition and sex ratios of spiky dogshark catches were similar for 1976–77 and 1996–97 (see Andrew *et al.* 1997). During both survey periods, catches off Sydney and Ulladulla consisted predominantly of females in the 50–60 cm TL size range, whereas the Eden catches comprised mostly males between 35 and 50 cm TL. The 1976–77 length data also suggested that catches off Sydney and

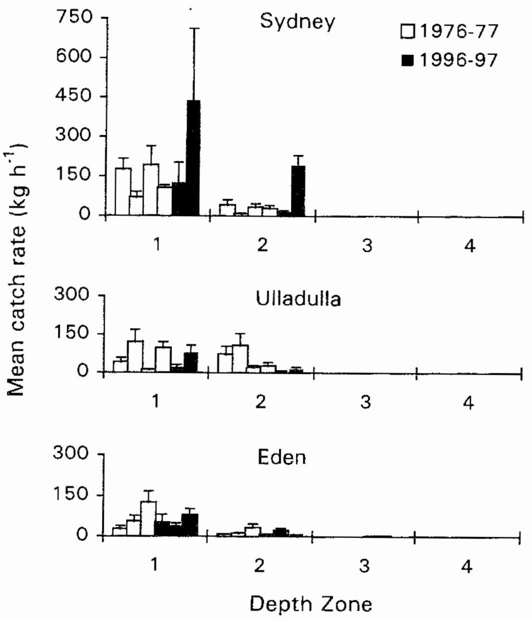


Fig. 10. Mean catch rates (kg h^{-1} + 1 s.e.) for spiky dogshark (*Squalus megalops*) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

Ulladulla included a small number of the larger *Squalus* sp. B. Five specimens of *Squalus* sp. B were caught in 1996 at these locations.

Eastern angel shark was caught in Zones 1 and 2 on all three grounds, but catches off Eden were relatively small (Fig. 11). In Zone 3, a total of 16 kg was caught during the 1976–77 surveys off Sydney and Ulladulla. Individual catches during the initial 1976 surveys were as high as 225 kg off Sydney and 320 kg off Ulladulla. Catches in subsequent 1976–77 surveys were generally much lower than this, except for those in Zone 2, Survey 4 off Ulladulla (Fig. 11). The overall mean catch rates on the Sydney and Ulladulla grounds (pooled for Zones 1 and 2) were 27 and 61 kg h^{-1}, respectively, in 1976–77, but less than 3 kg h^{-1} on each of the two grounds in 1996 (Table 1).

Small quantities of three valuable commercial species, gummy shark, eastern sawshark and school shark, were also caught, principally in Depth Zones 1 and 2 (Table 1). All three species showed reduced catch rates between the two sampling periods, although the differences for gummy and saw sharks were less marked off Sydney than for the other two grounds (Table 1). Only a single school shark was caught off Sydney in 1976–77 but they were common off Ulladulla and Eden, with individual catches as large as 100 kg. In 1996–97, no school sharks were caught on any ground.

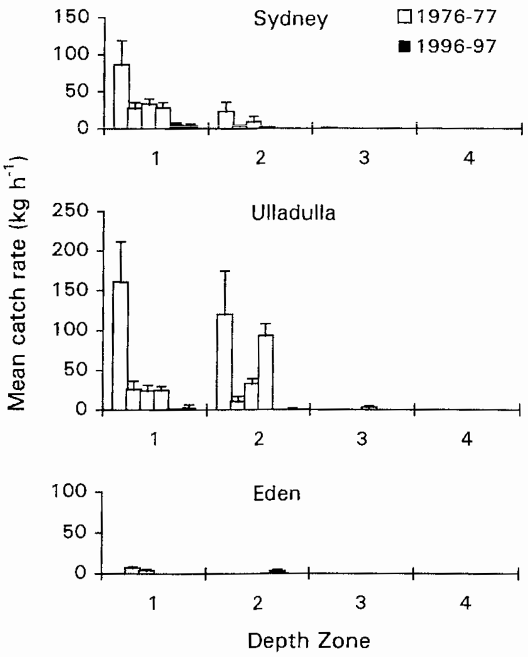


Fig. 11. Mean catch rates (kg h^{-1} + 1 s.e.) for eastern angel shark (*Squatina* sp. A) at each location. Each bar represents one survey. Depth zones are: 1, 200–275 m; 2, 330–385 m; 3, 440–495 m; 4, 550–605 m.

Four species of stingaree were caught in Zones 1 and 2. *Urolophus bucculentus* and *U. viridis* were commonly caught on all grounds; smaller quantities of *U. sufflavus* (Sydney) and *U. cruciatus* (Ulladulla and Eden) were present in some catches. Over 70% of the total stingaree catch during both survey periods was taken off Sydney (Table 1). Across Zones 1 and 2, the 1996 mean catch rate off Sydney was 45% lower than for 1976–77; average catches off Ulladulla and Eden were more than 80% lower.

In 1976–77, 45 of the 246 tows were done at night. The data from this relatively small number of tows suggest that the catchability of some species of dogsharks was greater at night, particularly in the shallower depths. Almost all Endeavour, Harrissons, southern and longsnout dogsharks caught in Depth Zone 1 were taken during night-time tows, although catch rates of these species in Zone 1 were comparatively low (Figs 3, 4 and 6). When data for Zones 2 and 3 were pooled, mean catch rates at night for Harrissons dogshark (55 kg h^{-1}) and longsnout dogshark (20 kg h^{-1}) were also greater than daytime catch rates (34 and 6 kg h^{-1}, respectively). Average catches of Endeavour and southern dogsharks were substantially greater during the day in Zones 2 and 3, and greater for all four species in Zone 4. For all other sharks and rays, daytime catch rates in all depths were similar to or greater than those at night.

Comparison with 1979–81 catch data

Comparative data for nine species were available from trawling done during 1979–81 on the 1976–77 and 1996–97 survey grounds, although within a more restricted depth range. Data were from 150 tows done in depths between 300 and 525 m and, for comparison, catch data were pooled for each of the three survey periods 1976–77, 1979–81 and 1996–97 (Table 2).

For total sharks and rays, the average 1979–81 catch rate on each of the three grounds was 35% (Sydney), 34% (Ulladulla) and 20% (Eden) of those in 1976–77 (Table 2). Individually, catch rates of all but whitefin swell shark were less than 50% of their 1976–77 levels, with three species of dogshark (southern, Endeavour and greeneye) less than 20%.

Discussion

The 1976–77 surveys of the Sydney, Ulladulla and Eden upper slope grounds were done close to the start of the NSW slope trawl fishery. Twenty years later, the 1996–97 mean catch rates of sharks and rays were, on average, approximately 20% of the 1976–77 levels. When spiky dogshark data are excluded, mean catches were less than 10% of those during the initial survey period. It is evident from the 1979–81 data that shark and ray abundance started changing during the early years of the fishery. During those surveys, average catch rates of total sharks and rays in 300–525 m were about one-third of the initial levels off Sydney

Table 2. Mean catch rates (kg h^{-1} and 1 s.e.) for species caught in tows between 300 and 525 m during 1976–77, 1979–81 and 1996–97

	Ground	1976–77		1979–81		1996–97	
No. of tows	Sydney	49		55		24	
	Ulladulla	47		36		24	
	Eden	34		59		33	
Species		kg h^{-1}	s.e.	kg h^{-1}	s.e	kg h^{-1}	s.e
Total shark & ray	All grounds	358.0	33.6	98.6	10.9	46.3	8.0
	Sydney	281.0	26.3	98.1	14.5	85.1	23.7
	Ulladulla	377.7	60.1	136.9	34.9	24.5	4.2
	Eden	441.7	90.0	90.0	12.4	34.0	6.0
Harrissons & southern dogsharks (combined)	All grounds	169.9	30.4	44.1	8.5	< 0.1	
	Sydney	59.5	13.4	44.9	12.3	< 0.1	
	Ulladulla	184.8	53.9	68.3	28.4	< 0.1	
	Eden	308.2	8.39	28.7	6.8	< 0.1	
Harrissons dogshark[A]	All grounds	37.6	6.9	17.4	4.2	< 0.1	
	Sydney	18.4	3.2	36.7	10.8	<0.1	
	Ulladulla	23.3	6.5	0.8	0.6	<0.1	
	Eden	65.8	16.2	9.5	2.8	0	
Southern dogshark[A]	All grounds	146.3	36.1	26.7	7.3	< 0.1	
	Sydney	31.4	6.7	8.2	2.7	0	
	Ulladulla	126.4	43.5	67.4	28.4	< 0.1	
	Eden	248.0	82.3	19.2	4.9	< 0.1	
Endeavour dogshark	All grounds	18.0	3.1	2.3	0.7	< 0.1	
	Sydney	35.4	6.4	6.3	1.9	0.3	0.2
	Ulladulla	13.0	4.5	0.1	0.1	0	
	Eden	0		0		0	
Greeneye dogsharks	All grounds	45.2	5.7	8.2	1.4	1.9	0.5
	Sydney	82.9	12.3	18.7	3.0	4.6	1.1
	Ulladulla	30.3	5.2	4.4	2.3	2.0	1.0
	Eden	11.5	3.7	0.6	0.3	<0.1	
Longsnout dogshark	All grounds	8.3	2.1	1.7	0.7	0.1	0.1
	Sydney	11.7	4.9	1.9	1.4	0	
	Ulladulla	5.4	1.8	1.6	1.0	0	
	Eden	7.5	3.2	1.7	0.9	0.3	0.2
Silver ghostshark	All grounds	11.9	1.9	3.5	0.7	0.3	0.1
	Sydney	9.5	2.7	3.8	1.6	0.8	0.3
	Ulladulla	3.4	1.0	0.8	0.3	0.3	0.2
	Eden	27.1	5.2	5.2	1.2	<0.1	
Whitefin swell shark	All grounds	8.6	1.1	6.5	0.9	7.0	1.7
	Sydney	7.1	3.4	1.6	0.6	1.8	0.4
	Ulladulla	9.9	1.3	7.1	2.6	2.9	1.0
	Eden	15.6	3.2	10.2	1.3	13.8	3.9
Skates	All grounds	48.6	5.0	21.7	2.6	6.5	1.1
	Sydney	47.8	6.7	12.8	2.7	10.9	3.9
	Ulladulla	53.7	10.9	32.4	7.6	3.4	1.1
	Eden	42.7	7.7	23.0	3.6	5.3	1.5
Sharpnose sevengill shark	All grounds	4.3	1.3	1.7	0.4	0.2	0.1
	Sydney	7.1	3.4	3.2	0.8	0.8	0.2
	Ulladulla	3.4	0.9	1.0	0.4	0	
	Eden	1.4	0.4	0.2	0.1	0	

[A] Data from tows when species was recorded separately.

and Ulladulla, and about 20% on the Eden ground. This was similar to the 70% decline in dogshark abundance between 1975 and 1982 documented from early *Kapala* upper slope surveys for deepwater prawns in the Sydney–Port Stephens area (Graham and Gorman 1985).

The greatest changes in abundance were for several species of sharks that are commercially valuable, whereas the two sharks that showed little appreciable change (spiky dogshark and whitefin swell shark) have relatively low market acceptance. Apart from whitefin swell shark, all species of sharks discussed in this study are marketed when larger than about 60 cm total length. The sharks are sold to the fresh fish trade, although the livers of some species (*Centrophorus* spp. and *Deania* spp.) are also valuable for their squalene oil content (Yearsley *et al.* 1999). Few, if any, shark fins are retained from species trawled off NSW. Although NSW trawlers land no stingaree and few skates, the abundances of these species were also markedly lower in 1996–97.

Dogsharks of the genus *Centrophorus* (Harrissons, southern and Endeavour) were almost absent from the 1996–97 catches. The very low catch rates by *Kapala* in 1996–97 off Ulladulla and Eden ($\leq$1.0 kg h^{-1}) were comparable with those reported for the commercial fleet at the time. Liggins (1996, 1997) estimated that the total annual catch of *Centrophorus* dogsharks by all Ulladulla and Eden trawlers off southern NSW averaged 19 t during the three years 1993–95, and 23 t for 1996, with a maximum mean catch rate of 24 kg per trawler-day. More recently, during September 1999–March 2000, only two Harrissons dogsharks and two southern dogsharks were caught during more than 60 hours of commercial trawling on the upper slope off the southern NSW port of Bermagui (K. Graham, personal observation). Of the large-sized species taken mainly in Depth Zones 1 and 2, comparatively few angel, saw or gummy sharks, and no school sharks were caught during 1996–97 off Ulladulla and Eden. Angel and saw sharks are caught principally by trawling but gummy and school sharks are also heavily fished by gill-net vessels in Bass Strait waters (Stevens *et al.* 1997; Walker 1999). This gill-net fishery possibly affects recruitment by these species onto the Ulladulla and Eden grounds. Off Sydney, greeneye dogsharks were most abundant in Zones 1 and 2 during 1976–77 but, along with angel shark, their 1996–97 catch rates were very low.

In contrast, spiky dogshark and whitefin swell shark abundances did not follow the general pattern of decline discussed above. Spiky dogsharks were most abundant off Sydney but, because of their relatively small size, fishers seldom target them. The few trawlers now operating on the slope off Sydney mainly fish for royal red prawns (*Haliporoides sibogae*) in depths between 400 and 550 m and only occasionally trawl between 200 and 400 m where sand lobsters (*Ibacus alticrenatus*) are often the principal target. It seems that the present level of trawling is sufficient to keep the numbers of the larger angel sharks and greeneye dogsharks comparatively low but not adversely affect spiky dogshark numbers. Spiky dogsharks are also abundant on the large area of outer shelf (120–200 m) between Wollongong and Newcastle (Graham *et al.* 1996). It is likely that spiky dogsharks readily recruit from this largely unfished area onto the adjacent upper slope grounds, helping to maintain their overall biomass. Off Ulladulla and Eden there is much more intense trawler activity on both the outer shelf and upper slope with teleost fishes (mainly redfish) the main targets. On both these grounds, spiky dogshark was less abundant than off Sydney and, although the 1996–97 mean catch rates were not significantly different from those in 1976–77 (Andrew *et al.* 1997), they were lower. The fact that the 1996 Ulladulla mean catch rate was less than half that in 1976–77 may suggest that the relatively heavy fishing pressure off that port is beginning to affect local spiky dogshark abundance.

Whitefin swell shark was the only species caught in all depths that had similar average catch rates during the three survey periods (1976–77, 1979–81 and 1996–97). The mean catch rate across all grounds in 1996–97 was only about 30% lower than in 1976–77, and for the depth range 300–525 m catch rates were almost equal for each of the three survey periods. This species has very low commercial value and is usually discarded by trawlers. It is one of the few species that survives capture (K. Graham, personal observation) and seems likely to live if quickly returned to the sea.

The differences in catch rates among survey periods were not confounded by diurnal differences in availability. Although the 1976–77 catch rates of a number of dogsharks were greater at night in some depths, particularly in Zone 1, their abundance in these depths was comparatively low. However, substantial catches of all species were taken during the day in most depth zones, and for almost all species, daytime catch rates were greater than or equivalent to catch rates from the small number of night-time tows. Overall, changes among survey periods were consistent among all depth zones regardless of whether catch rates were greater during the day or night.

Almost all trawlable ground on the slope off NSW (and probably the whole of SE Australia) is regularly fished, maintaining continual fishing pressure on the sharks and rays that inhabit these grounds. Although the high catch rates in 1976–77 suggest that many species of demersal shark can be abundant over trawlable substrate, little is known about their distribution and abundance in non-trawlable areas. About 25% of the total area of seabed on the NSW upper slope between Newcastle and the Horseshoe is untrawlable because of canyons or ‘foul’ ground. Dropline fishers target blue-eye (*Hyperoglyphe antarctica*) on some of these rough bottom areas; annual landings of dogsharks, mainly *Centrophorus* spp., reported by dropliners for the years 1994–1998 ranged between 1.8 and 5.7 t (NSW Fisheries Catch Data). Although these catches appear small, there are no data for the 1970s and so we have no way of knowing whether there have been changes through time in the relative abundance of dogsharks on non-trawlable ground.

The impact of trawling on the biomass of NSW slope sharks and rays appears to have followed the pattern of most exploited demersal shark stocks worldwide (see case studies reported in Shotton (1999) for a recent compilation). The susceptibility of chondrichthyans to fishing pressure and, frequently, stock collapse has been widely reported in the literature (Holden 1974; Anderson 1990; Compagno 1990; Hoenig and Gruber 1990; Pratt and Casey 1990; Stevens *et al.* 1997; Walker 1998) and is inextricably related to their biology. Life history attributes that predispose sharks and rays to overexploitation include slow growth, late onset of sexual maturity, oviparous, ovoviviparous or viviparous reproduction, low fecundity, and low natural mortality. The species sampled during this study possess many of these characteristics. Biological information collected on NSW slope dogsharks (K. Graham, unpublished) shows that all species reach maturity when they are close to their maximum size. The southern dogshark produces only a single pup at any time and Harrissons dogshark bears one or, more commonly, two pups. Spiky dogshark has a maximum litter size of three, and of the two greeneye dogshark species, up to 10 pups were observed in *Squalus mitsukurii*, and up to five in *Squalus* sp. F. Gestation time is unknown for these species in Australian waters but is likely to be between one and two years, the usual time for squaloid sharks (Ketchen 1972; Hanchet 1988; Yano and Tanaka 1988; Wilson and Seki 1994). Gordon (1999) suggests that the gestation period of some deepwater squalids could be as long as two to three years. Age at sexual maturity is unknown for Australian dogsharks but Watson and Smale (1999) estimated that for the South African spiny dogshark (*S. megalops*), females take (on average) 22 years to mature, and males 15 years. It is likely that the larger species of dogsharks on the NSW slope mature at an even greater age. The low fecundity of the NSW slope chondrichthyans was reflected in the catch composition. Unlike some species of teleosts that had substantially reduced numbers of large fish but relatively high numbers of juveniles (Andrew *et al.* 1997), very few juvenile sharks and rays were caught during 1996–97. It is most likely, therefore, that the regular fishing pressure of the SEF trawl fleet combined with the life history attributes of these species will ensure that the stocks remain at low levels.

In summary, we believe there is a strong basis for inferring that sustained trawling over 20 years is the most likely and predominant cause of the observed changes in relative abundance of sharks and rays on the NSW upper slope. This interpretation relies on combining relative abundance data from three time periods in the fishery with knowledge of the history of the fishery and the biology of these species. When all the data are considered, the magnitude and consistency of the decline among sampling periods, surveys and replicate tows suggest that the observed patterns reflect real changes. The very low relative abundances described in this study further suggest that stocks are at historically low levels. As confirmed by Liggins (1996, 1997), sharks are now only a minor component of the commercial catch from the NSW upper slope. However, there are currently no management measures for any chondrichthyans caught by trawling in the SEF. When catch quotas were introduced for 15 species of teleosts in 1992 (Tilzey 1994), sharks were already a minor component of the commercial catch. Teleost fishes continue to sustain the trawl sector of the SEF and there are no stock assessments for commercial sharks. This lack of management for sharks is consistent with Bonfil's (1994) suggestion that few managers will constrain economically or socially important fisheries to manage elasmobranch stocks.

Last and Steven's (1994) guide to the Australian chondrichthyan fauna includes 97 species not identifiable in the literature. At least half of the undescribed species were reported from slope depths, highlighting the relative lack of knowledge about Australia's deepwater fauna. Many of the species caught on the NSW slope appear to have restricted natural distributions and some species such as Harrissons dogshark, eastern sawshark and Grahams skate (*Raja* sp. C) are found only off NSW and eastern Bass Strait (Last and Stevens 1994). Harrissons dogshark was also reported from Western Australia but that population is now considered distinct from the east coast species (P. Last, personal communication). The large size, low fecundity (see above) and relatively high commercial value of Harrissons dogshark make this and similar species particularly vulnerable. If sharks and rays are considered important components of the biodiversity of the outer continental shelf and upper slope, then conservation measures need to be quickly canvassed. Management measures appropriate to multispecies fisheries such as the SEF include closing sections of the fishing grounds to trawling (see also Bax *et al.* 1999). Replicated closures along the NSW coast would provide the basis for a large-scale evaluation of the efficacy of this management option (Walters 1986; Bohnsack 1990; McAllister and Peterman 1992; Sainsbury *et al.* 1997; Sumaila 1998).

Acknowledgments

We gratefully acknowledge Terry Gorman's 20-year contribution to the successful operation of FRV *Kapala*. The masters and crew of *Kapala* are also thanked for facilitating and completing the surveys reported here. We thank Bob

Kearney and Richard Tilzey for support in the early stages of the project and Geoff Liggins for his advice and discussion. Ric Fletcher, David Pollard and Kevin Rowling reviewed the manuscript. This study was funded by NSW Fisheries and the Fisheries Research and Development Corporation (Project 96/139).

References

Anderson, E. D. (1990). Fishery models as applied to elasmobranch fisheries. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and Status of the Fisheries', 9–14 December 1987. East–West Center, Honolulu, Hawaii. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) NOAA Technical Report NMFS 90. pp. 473–84. (US Department of Commerce.)

Andrew, N. L., Graham, K. J., Hodgson, K. E., and Gordon, G. N. G. (1997). Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. FRDC Project No. 96/139. NSW Fisheries Final Report Series No. 1. 109 pp. (NSW Fisheries Research Institute: Cronulla, Australia.)

Bax, N., Williams, A., Davenport, S., and Bulman, C. (1999). Managing the ecosystem by leverage points: a model for a multispecies fishery. In 'Ecosystem Approaches for Fisheries Management'. Alaska Sea Grant College Program. pp. 283–304.

Bohnsack, J. (1990). The potential of marine fishery reserves for reef fish management in the US Southern Atlantic. NOAA Technical Memorandum NMFS-SEFC-261, 40 pp.

Bonfil, R. (1994). Overview of world elasmobranch fisheries. FAO Fisheries Technical Paper No. 341. 119 pp.

Compagno, L. J. V. (1990). Shark exploitation and conservation. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and Status of the Fisheries', 9–14 December 1987. East-West Center, Honolulu, Hawaii. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) NOAA Technical Report NMFS 90. pp. 391–414. (US Department of Commerce.)

Crozier, N. and Graham, K. J (1978). Development of NSW offshore fish resources. *Australian Fisheries* **37**, 4–9.

Diorio, A. (1976). NSW trawling: 1938–1974. In 'Proceedings of the 1974 Trawling Seminar held by NSW State Fisheries, Sydney, October 14th–18th 1974'. pp. 111–13. (Government Printer: New South Wales.)

Gordon, J. D. M. (1999). Management considerations of deep-water shark fisheries. In 'Case Studies of the Management of Elasmobranch Fisheries'. (Ed. R. Shotton.) pp. 774–818. FAO Fisheries Technical Paper No. 378.

Graham, K. J., and Gorman, T. B. (1985). New South Wales deepwater prawn fishery research and development. In 'Second Aust. Nat. Prawn Sem.' (Eds P. C. Rothlisberg, B. J. Hill and D. J. Staples.) pp. 231–43. (NPS2: Cleveland, Australia.)

Graham, K. J., Winstanley, R. H., and Wilson, M. A. (1982). Fishery Situation Report 9. Trawl and Danish seine fishery. Published for South Eastern Fisheries Committee by CSIRO Laboratories, Australia. 31 pp.

Graham, K. J., Liggins G. W., and Wildforster, J. (1996). New South Wales continental shelf survey results for year 2: 1994. Kapala Cruise Report No. 115. (NSW Fisheries Research Institute: Cronulla Australia.) 63 pp.

Graham, K. J., Wood, B. R., and Andrew, N. L. (1997). The 1996–97 survey of upper slope trawling grounds between Sydney and Gabo Island (and comparisons with the 1976–77 survey). Kapala Cruise Report No. 117. (NSW Fisheries Research Institute: Cronulla Australia.) 96 pp.

Hanchet, S. (1988). Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **22**, 537–49.

Hoenig, J. M., and Gruber, S. H. (1990). Life-history patterns in elasmobranchs: implications for fisheries management. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and Status of the Fisheries', 9–14 December 1987. East-West Center, Honolulu, Hawaii. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) NOAA Technical Report NMFS 90. pp. 1–16. (US Department of Commerce.)

Holden, M. J. (1974). Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In 'Sea Fisheries Research'. (Ed. F. R. Harden-Jones.) pp. 117–37. (John Wiley: New York.)

Ketchen, K. S. (1972). Size at maturity, fecundity and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbian waters. *Journal of the Fisheries Research Board of Canada* **29**, 1717–23.

Last, P. R. and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' 513 pp. (CSIRO Australia: Melbourne.)

Liggins, G. W. (1996). The interaction between fish trawling (in NSW) and other commercial and recreational fisheries. Final Report to the Fisheries Research and Development Corporation. (NSW Fisheries Research Institute: Cronulla, Australia.)

Liggins, G. W. (1997). Integrated scientific monitoring program for the SEF in 1996 (NSW component). Report to Australian Fisheries Management Authority. (NSW Fisheries Research Institute: Cronulla, Australia.)

McAllister, M. K. and Peterman, R. M. (1992). Experimental design in the management of fisheries. *North American Journal of Fisheries Management* **12**, 1–18.

Pratt, H. L. Jr, and Casey, J. G. (1990). Shark reproduction strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth-parameters. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and Status of the Fisheries', 9–14 December 1987. East–West Center, Honolulu, Hawaii. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) NOAA Technical Report NMFS 90. pp. 97–109. (US Department of Commerce.)

Rowling, K. R. (1994a). Gemfish, *Rexea solandri*. In 'The South East Fishery'. (Ed. R. D. J. Tilzey.) pp.115–23. (Bureau of Resource Sciences: Canberra.)

Rowling, K. R. (1994b). Redfish, *Centroberyx affinis*. In 'The South East Fishery'. (Ed. R. D. J. Tilzey.) pp. 149–58. (Bureau of Resource Sciences: Canberra.)

Rowling, K. R. (1997). The collapse of the eastern Australian gemfish stock – issues for management and the role of fisheries science. In 'Developing and Sustaining World Fisheries Resources: the State of Science and Management. Second World Fisheries Congress' 28 July–2 August 1996, Brisbane. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. P. Beumer.) pp. 210–19. (CSIRO Publishing: Melbourne.)

Sainsbury, K. J., Campbell, R. A., Lindholm, R., and Whitelaw, A. W. (1997). Experimental management of an Australian multispecies fishery: examining the possibility of trawl-induced habitat modification. In 'Global Trends: Fishery Management'. (Eds E. K. Pikitch, D. D. Huppert and M. P. Sisssenwine.) pp. 107–12. American Fisheries Society Symposium 20. (Bethesda, MD.)

Shotton, R. (Ed.) (1999). Case studies of the management of elasmobranch fisheries. FAO Fisheries Technical Paper. No. 378. 920 pp. (FAO: Rome.)

Stevens, J. D., Walker, T. I., and Simpfendorfer, C. A . (1997). Are southern Australian shark fisheries sustainable? In 'Developing and Sustaining World Fisheries Resources: the State of Science and

Management. Second World Fisheries Congress' 28 July–2 August 1996, Brisbane. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. P. Beumer.) pp. 62–6. (CSIRO Publishing: Melbourne.)

Sumaila, U. R. (1998). Protected marine reserves as fisheries management tools: a bioeconomic analysis. *Fisheries Research* **37**, 287–96.

Tilzey, R. D. J. (Ed.) (1994). 'The South East Fishery'. (Bureau of Resource Sciences: Canberra.) 360 pp.

Walker, T. I. (1998). Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* **49**, 553–72.

Walker, T. I. (1999). Southern Australian shark fishery management. In 'Case Studies of the Management of Elasmobranch Fisheries'. (Ed. R. Shotton.) FAO Fisheries Technical Paper No. 378. 920 pp. (FAO: Rome.)

Walters, C. J. (1986). 'Adaptive Management of Renewable Resources.' (Macmillan: New York.)

Watson, G., and Smale, M. J. (1999). Age and growth of the shortnose spiny dogfish *Squalus megalops* from the Agulhas Bank, South Africa. *South African Journal of Marine Science* **21**, 9–18.

Wilson, C. D., and Seki, M. P. (1994). Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central North Pacific Ocean. *Fishery Bulletin US* **92**, 851–64.

Yano, K., and Tanaka, S. (1988). Size at maturity, reproductive cycle, fecundity, and depth segregation of the deep sea squaloid sharks *Centroscymnus owstoni* and *C. coelolepis* in Suruga Bay, Japan. *Nippon Suisan Gakkaishi* **54**, 167–74.

Yearsley, G. K., Last, P. R., Ward, R. D. (1999). 'Australian Seafood Handbook: an Identification Guide to Domestic Species.' 461 pp. (CSIRO Marine Research: Australia.)

Manuscript received 26 November 1999; revised and accepted 7 June 2000

Mar. Freshwater Res., 2001, **52**, 563–73

Genetic population structure of species in the South East Fishery of Australia

R. D. Ward and N. G. Elliott

CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia. email: Bob.Ward@marine.csiro.au

Abstract. A summary is given of allozyme, mitochondrial DNA and microsatellite data for commercially important species (13 fish and 7 shellfish) in Australia's South East Fishery, including contiguous waters and the Tasman Sea. For most fish species, genetic population differentiation was limited and in about half the studies was non-detectable. Striking population differentiation was recorded for gemfish. For fish species, on average only 2–3% of the total genetic variation could be attributed to population differentiation within southern Australian waters. In shellfish, ~5% of variation arose from population differences. The reduced differentiation of fish populations may be due to a longer larval period and greater adult mobility. Although there was evidence that the Tasman Sea acts as a barrier to gene flow, with most fish species showing significant differences between Australia and New Zealand, the degree of differentiation was small (only ~2%). The limited genetic differentiation observed for most species is attributable to the lack of major oceanographic and environmental barriers to gene flow, together with influential current systems; it necessitates large sample sizes for good genetic tests. However, significant genetic stock structuring is apparent for several fish and shellfish species – particularly for coastal species, where isolation by distance may explain some of the data. Any evidence for genetic stock structure must be factored into plans for sustainable management.

Introduction

The South East Fishery (SEF) of Australia is one of Australia's principal fisheries, with an annual commercial catch of over 24000 tonnes and a value of more than $55 million per year. It is a multispecies fishery including a wide variety of fish species and some invertebrates (prawns, squid). The SEF fishing zone extends from 3 nautical miles to the 200 nautical mile limit of the Australian Exclusive Economic Zone around south-eastern Australia, from Barranjoey Point in New South Wales (33°35'S) to Cape Jervis in South Australia (138°08'E), including offshore waters of Victoria and Tasmania (Fig. 1).

The mode of management of species within this fishery varies according to species. The 21 major species of the trawled sector (Table 1) have been managed since 1992 by Individual Transferable Quotas (ITQ) based on Total Allowable Catches (TAC). These quota species have at least 65 non-quota relatives, and a recent publication was aimed at assisting the correct identification of these 85 or so species (Daley *et al.* 1997). Yearsley *et al.* (1999) describes both trawl and non-trawl commercial fish and shellfish species found throughout Australia. Both books include protein fingerprints of all species.

A primary objective of fisheries management is to ensure sustainability of the resource, while simultaneously taking into account economic, social and sometimes political factors. The scientific data required include, primarily, stock abundance and productivity estimates, and information on stock dynamics. A recent review of stock assessment methods (Deriso and Quinn 1998) included as number one in a recommended check list of items, information on spatial distribution or stock structure. It suggested that such information could be garnered from tagging, microconstituents of hard parts (e.g. otoliths), genetics and/or morphometrics. Ward (2000) has briefly outlined the various uses of genetics in fisheries management, and Grant *et al.* (1999) and Carvalho and Hauser (1994) have reviewed genetic applications to defining stock boundaries.

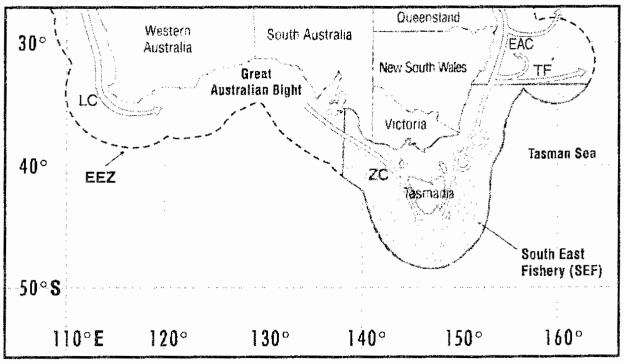


Fig. 1. Map of southern Australian waters, including the South East Fishery and the schematic representation of the major currents (G. Cresswell, personal communication). LC, Leeuwin Current; ZC, Zeehan Current; EAC, East Australian Current; TF, Tasman Front. The line indicated as EEZ delimits Australia's Exclusive Economic Zone.

10.1071/MF99184 1323-1650/01/040563

Table 1. List of South East Fishery quota species, indicating whether there are genetic data available (–, a, m and o indicate no data, allozyme data, mtDNA data and nuclear DNA data, respectively) and whether there is evidence for genetic structure (– indicates no data, yes and no indicates positive or no evidence for differentiation, respectively)

Common name	Scientific name	Genetic data	Genetic structuring?	
			Southern Australia	Trans-Tasman
John dory	*Zeus faber*	–	–	–
Mirror dory	*Zenopsis nebulosus*	–	–	–
Tiger flathead	*Neoplatycephalus richardsoni*	–	–	–
Toothy flathead	*Neoplatycephalus aurimaculatus*	–	–	–
Sand flathead	*Platycephalus bassensis*	–	–	–
Bluespot flathead	*Platycephalus caeruleopunctatus*	–	–	–
Southern flathead	*Platycephalus speculator*	–	–	–
Gemfish	*Rexea solandri*	a, m	yes	yes
Blue grenadier	*Macruronus novaezelandiae*	a	yes	yes
Pink ling	*Genypterus blacodes*	a, o	no	–
Jackass morwong	*Nemadactylus macropterus*	a, m	no	yes
Ocean perch	*Helicolenus* species[A]	–	–	–
Royal red prawn	*Haliporoides sibogae*	–	–	–
Redfish	*Centroberyx affinis*	–	–	–
Orange roughy	*Hoplostethus atlanticus*	a, m, o	yes	yes
Silver trevally	*Pseudocaranx dentex*	–	–	–
Blue eye	*Hyperoglyphe antarctica*	a	no	–
Blue warehou	*Seriolella brama*	–	–	–
Silver warehou	*Seriolella punctata*	–	–	–
Eastern school whiting	*Sillago flindersi*	–	–	–

[A] Two species.

Marine fish often show high gene flow, leading to limited population differentiation in comparison with freshwater species (Ward *et al.* 1994). Free-swimming adult marine fish have few physical barriers to movement, and there may be extensive egg or larval dispersal in ocean currents. In fact, current systems facilitate movement of all life history stages. The major current systems of south-eastern Australia are the south-easterly flowing waters of the Zeehan Current from the Great Australian Bight and the southerly flowing warm waters of the East Australian Current (Fig. 1). In addition, the SEF region contains the shallower waters of Bass Strait with little through-flow of water but significant tidal influence; it is a historical boundary for species during periods of low seawater levels. Circulation within the Tasman Sea to the east of the SEF has the potential to link marine fauna of Australia and New Zealand. There are, however, no major physical features that mark the boundaries to the SEF and that might play a role in restricting migration into or out of the region. All quota species in the SEF have distribution ranges that extend outside the management boundaries of the fishery; spawning sites may be inside and/or outside these boundaries.

Here we will review how genetic studies have contributed towards a deeper understanding of the population structure of species within the SEF and contiguous waters. We do not restrict ourselves to quota species, but also consider other species taken in this region, including some inshore species. Most of the species are fish, but a number of commercially important molluscs and crustaceans are also included.

Genetic techniques for examining population structure

Genetic approaches to determining population structure all rely on partitioning genetic variation into within- and between-population components. If there is a restriction to gene flow between populations, then the between-population component will be larger than that attributable to chance.

Genetic variation can be assessed by one of a variety of approaches. The most common technique has been allozyme electrophoresis, which quantifies the extent of genetically determined electrophoretic variation of proteins. This reflects nuclear DNA variability. Perhaps the next most common approach has been to assess the degree of mitochondrial DNA (mtDNA) variability; this is a small (~16 kb) circular DNA molecule housed within mitochondria and solely inherited maternally (with very rare exceptions). More recently, attention has focussed on the analysis of microsatellite nuclear DNA (analysing variation in the number of tandem repeats of one to four nucleotide base repeat motifs, that are generally less than 300 bp in length). These techniques and their advantages and disadvantages for fisheries analysis are described elsewhere (e.g. Park and Moran 1994; Ward and Grewe 1994; O'Connell and Wright 1997).

For this review, Nei's (1973) gene diversity (G_{ST}) statistics were generally used to quantify the extent of

Table 2. Non-SEF quota species considered herein, indicating what genetic data are available (a, m and o indicate allozyme data, mtDNA data and nuclear DNA data, respectively) and whether there is evidence for genetic structure (– indicates no data, yes and no indicate positive or no evidence for differentiation, respectively)

Common name	Scientific name	Genetic data	Genetic structuring?	
			Southern Australia	Trans-Tasman
Smooth oreo	*Pseudocyttus maculatus*	a, m	no	no
Warty oreo	*Allocyttus verrucosus*	a, m	yes	–
Spikey oreo	*Neocyttus rhomboidalis*	a, m	yes	yes
Black oreo	*Allocyttus niger*	a, m	–	no
Gummy shark	*Mustelus antarcticus*	a, m	no	–
School shark	*Galeorhinus galeus*	a, m	no	yes
Jack mackerel	*Trachurus declivis*	a, m	yes	–
Greenback flounder	*Rhombosolea tapirina*	a	yes	yes
Clam	*Katelysia scalarina*	a	yes	–
Clam	*Ruditapes largillierti*	a	–	no
Blacklip abalone	*Haliotis rubra*	a, m, o	yes	–
Greenlip abalone	*Haliotis laevigata*	a	yes	–
Southern rock lobster	*Jasus edwardsii*	a, m	yes	yes
Eastern rock lobster	*Jasus verreauxi*	m	–	yes
Scallop	*Pecten fumatus*	a	yes	–

differentiation among collections. G_{ST} is equal to $(H_T–H_S)/H_T$, where H_T (total genetic diversity) is the Hardy-Weinberg expected heterozygosity estimated from the allele frequency in the total sample, and H_S is the average Hardy-Weinberg expected heterozygosity within collections. For mtDNA, haplotype diversity may be substituted for heterozygosity. Across all loci, G_{ST} was estimated from the mean of the H_T and H_S values. The G_{ST} value represents the proportion of genetic diversity that can be attributed to differences between collections. It is operationally very similar to Wright's F_{ST} statistic, and the two parameters are used interchangeably here. Here its significance has been usually assessed by comparison with stochastic or sampling error. Many published data sets have been re-analysed for this review, as often the analyses performed by the authors were not in the format we preferred.

Genetic studies of species within the SEF

Table 1 lists the SEF quota species and indicates which have been subject to genetically based population structure analyses; non-quota species covered in this review are listed in Table 2. Studies of allozyme and mtDNA variation in species occupying the SEF (and contiguous waters) are summarized in Tables 3 and 4, respectively. In this region, microsatellite data are thus far restricted to pink ling, orange roughy and abalone. We will first discuss individual species before going on to draw some general conclusions.

Gemfish

Two distinct genetic stocks of *Rexea solandri* are evident across southern Australia (Colgan and Paxton 1997). Allozyme analysis revealed that nearly 20% of the variation at five variable allozyme loci was attributable to population differentiation, a much higher percentage than that attributable to stochastic error (Table 3). Much of this was due to the locus *AAT-2**, which alone had a G_{ST} value of close to 60%. Allele *AAT-2*C* had a frequency of ~75% in South Australia, the Great Australian Bight and (southern) West Australia, but was absent from New South Wales and eastern Tasmanian sites and at a low frequency of 0.25 in western Tasmania. The samples were also subjected to mtDNA analysis, although not all samples were assayed with the full range of 11 restriction enzymes and indeed some fish were only scored for a single restriction enzyme. Nonetheless, nearly all the detected mtDNA variation arose from population differentiation (G_{ST} ~96%; Table 4), with the South Australia, Great Australian Bight and Western Australia samples being monomorphic for a haplotype absent from other collections. Colgan and Paxton (1997) concluded that there is an eastern Australian stock (including much of the SEF region) and a southern/western stock, with limited mixing off western Tasmania.

Blue grenadier

A large-scale allozyme survey of *Macruronus novaezelandiae* was carried out within the SEF, with samples from around Tasmania, eastern Victoria and southern New South Wales (Milton and Shaklee 1987). Only ~0.7% of the variation arose from sample differences, although given the large sample sizes this proportion was significantly greater than that expected of sampling error (Table 3). This differentiation reflected small temporal rather than spatial differences, and the authors conclude that, in the absence of indications to the contrary, south-eastern Australian fish can be treated as a single interbreeding unit.

Table 3. The allozyme population structure of species in southern Australian waters (New Zealand samples excluded)

Species	Number Populations^A	Loci	Sample size per locus^B	Polymorphism (0.95 criterion)	Heterozygosity	G_{ST}^{C}	P^D	Reference
Gemfish	5 SEF, 1 NSW, 1 GAB, 1 WA	36	124–222	0.139	0.050	0.192 (5)	<0.001	Colgan and Paxton 1997
Blue grenadier	21 SEF	46	300–1715	0.174	0.068	0.007 (10)	<0.001	Milton and Shaklee 1987
Pink ling	5 SEF	38	10–357	0.237	0.075	0.011 (3)	n.s.	Daley and Ward, unpublished
Jackass morwong	6 SEF, 1 GAB, 1 WA	33	109–658	0.242	0.101	0.005 (8)	n.s.	Elliott and Ward 1994
Jackass morwong	10 SEF	5	748–1020	–	?	0.020 (4)	n.s.	Richardson 1982*b*
Orange roughy	5 SEF	9	423–530	–	?	0.023 (9)	<0.001	Black and Dixon 1989
Orange roughy	4 SEF, 1 GAB, 1 WA	28	722–724	0.393	0.130	0.005 (11)	n.s.	Elliott and Ward 1992
Blue-eye trevalla	6 SEF	36	146–681	0.139	0.053	0.004 (36)	n.s.	Bolch *et al.* 1993
Smooth oreo	1 SEF, 1 WA	29	224–315	0.276	0.110	0.001 (29)	n.s.	Ward *et al.* 1998
Warty oreo	2 SEF, 1 WA	25	167–312	0.320	0.140	0.013 (8)	0.003	Ward *et al.* 1998
Spikey oreo	6 SEF, 1 GAB, 1 WA	28	398–859	0.393	0.130	0.074 (11)	<0.001	Elliott *et al.* 1998
Jack mackerel	8 SEF, 3 WA	6	603–793	–	?	0.022 (6)	0.001	Richardson 1982*a*
Gummy shark	5 SEF, 2 GAB, 1 WA	27	121–358	0.185	0.086	0.034 (27)	n.s.	Gardner and Ward 1998
Greenback flounder	6 SEF	30	56–100	0.233	0.080	0.024 (30)	<0.001	van den Enden *et al.* 2000
Venerid clam	4 SEF, 1 GAB, 1 WA	6	58–120	0.719^E	0.316^E	0.086 (6)	<0.001	Soh *et al.* 1998
Blacklip abalone	14 SEF, 2 GAB, 1 WA	15	1431	0.533	0.143	0.033 (15)	<0.001	Brown 1991
Southern rocklobster	3 SEF	1	165	–	0.281	0.063 (1)	<0.001	Booth *et al.* 1990
Scallop	15 SEF	17	231–1672	0.706	0.314	0.030 (12)	–	Woodburn 1989

n.s., not significant. ^{A} SEF, South East Fishery; NSW, (mid-north) New South Wales; GAB, Great Australian Bight; WA, (south) Western Australia. ^{B} Where there is a large range, sample size is generally at or near maximum for polymorphic loci. ^{C}Number in parentheses is number of loci used for G_{ST} analysis. When less than number of loci examined, it usually includes the most variable loci only. ^{D} Probability of the G_{ST} value being larger than that attributable to sampling error alone. ^{E} Estimates from two populations examined for 16 loci.

Table 4. The mtDNA population structure of species in southern Australian waters (New Zealand samples excluded)

Species	Populations^A	Restriction enzymes^B	Sample size	Haplotype diversity	Nucleotide diversity (%)	G_{ST}	P^C	Reference
Gemfish	5 SEF, 1 NSW, 1 GAB, 1 WA	1–11	69	0.488	?	0.963	<0.001	Colgan and Paxton 1997
Jackass morwong	5 SEF, 1 GAB, 1 WA	9	166	0.671	0.458	0.035	n.s.	Grewe *et al.* 1994
Jackass morwong	6 SEF, 1 GAB, 1 WA	3	429	0.647	1.145	0.020	n.s.	Grewe *et al.* 1994
Orange roughy	5 SEF	3 (4bc)	79	0.998	0.665	0.061	n.s.	Smolenski *et al.* 1993
Orange roughy	9 SEF, 1 GAB	10 (6bc)	293	0.327	0.126	0.062	n.s.	Smolenski *et al.* 1993
Smooth oreo	1 SEF, 1 WA	2	186	0.578	0.960	0.008	n.s.	Ward *et al.* 1998
Warty oreo	2 SEF, 1 WA	2	162	0.169	0.350	0.020	n.s.	Ward *et al.* 1998
Spikey oreo	1 SEF, 1 LHR	10	170	0.750	?	0.009	n.s.	Elliott *et al.* 1998
Spikey oreo	5 SEF, 2 GAB, 1 WA	2	565	0.684	?	0.016	n.s.	Elliott *et al.* 1998
Jack mackerel	4 SEF	11 (6bc)	75	0.393	0.136	0.082	0.045	Smolenski *et al.* 1994
Jack mackerel	4 SEF	4 (4bc)	42	0.986	0.515	0.080	n.s.	Smolenski *et al.* 1994
Gummy shark	5 SEF, 2 GAB, 1 WA	6	371	0.473	?	0.040	n.s.	Gardner and Ward 1998
Southern rock lobster	9 SEF, 1 GAB, 1 WA	6	113	?	?	0.095	n.s.	Ovenden *et al.* 1992

n.s., not significant. ^{A} SEF, South East Trawl Fishery; NSW, (mid-north) New South Wales; GAB, Great Australian Bight; WA, (south) Western Australia. ^{B} Number of enzymes used; 4bc, four base recognizing restriction enzymes; 6bc, six base recognizing restriction enzymes. ^{C} Probability of the G_{ST} value being larger than that attributable to sampling error alone.

Pink ling

Three polymorphic allozymes were assayed in five SEF samples of *Genypterus blacodes*, from New South Wales to eastern Tasmania. No significant spatial differences were found (Table 3). The samples were also examined for nine microsatellite loci (Ward and Reilly 2001). These had 11–52 alleles per locus and Hardy-Weinberg-observed heterozygosities ranged from 0.55 to 0.95. No significant spatial differentiation was detected. Shallow-water fish (typically orange in colour) and deep-water fish (the normal pink colour) cannot be genetically differentiated with allozymes or microsatellites; they are clearly different forms of the same species. On the other hand, the rock ling (*G. tigerinus*) is allozymically quite distinct. The null hypothesis of a single panmictic population of pink ling in the SEF cannot be rejected. For details see Ward *et al.* (2001).

Jackass morwong

There have been two allozyme surveys of *Nemadactylus macropterus* in this region. The first (Richardson 1982*b*) examined samples from the SEF for five loci, but only four were typed in all collections. The observed G_{ST} value for these four loci was ~2% (Table 3), not quite significantly larger than that attributable to sampling error alone ($P = 0.055$). The second survey (Elliott and Ward 1994) examined more loci from a wider region (from Western Australia to New South Wales, and including the SEF), but total sample sizes were smaller than the earlier survey. The observed G_{ST} value (from eight polymorphic loci) was 0.005 (less than 1%), again not significantly larger than that attributable to sampling error. Two mtDNA analyses were carried out (Grewe *et al.* 1994). One of these analyses examined a total of 166 fish for composite haplotypes following restriction digests with nine enzymes, and a second analysis examined 429 fish with three enzymes known to detect polymorphic sites. Neither of these analyses detected spatial heterogeneity (Table 4). All three studies (Richardson 1982*b*; Elliott and Ward 1994; Grewe *et al.* 1994) concluded that there was no evidence of genetic population structuring for jackass morwong in southern Australian waters.

Orange roughy

There have been more genetic studies of *Hoplostethus atlanticus* in Australian (and New Zealand) waters than of any other species, reflecting its importance in the fishery. The first Australian allozyme study was that of Black and Dixon (1989). They examined nine polymorphic loci in five SEF samples (from Kangaroo Island to southern New South Wales), and concluded that there were two subpopulations in this region: South Australia, and Tasmania and eastern Australia. While six of the nine loci showed significant differentiation ($P<0.015$ to $P<0.001$) across the samples, the subpopulations were primarily differentiated by one locus. At this locus, *ME**, an allele present in frequencies greater than 0.5 in all other Australian samples (0.56–0.64; New Zealand was 0.69), had a frequency of only 0.24 in South Australia. The overall G_{ST} value was 0.023, greater than that attributable to chance ($P<0.001$). If *ME** is removed, the G_{ST} value falls to 0.013, still more than that expected from chance ($P<0.001$). Three enzymes (IDH, MDH, ME) in this study gave anomalous banding patterns in heterozygotes, inconsistent with known quaternary structures (Ward *et al.* 1992). The second Australian study was that of Elliott and Ward (1992). They examined 11 polymorphic loci in four SEF samples (from southern Tasmania to New South Wales) plus one sample from the Great Australian Bight and one from Western Australia. No anomalous heterozygote banding patterns were observed. Only one of the 11 loci showed differentiation ($P = 0.04$, non-significant after Bonferroni correction for multiple tests). No significant spatial differentiation was detected over all samples and loci ($G_{ST} = 0.005$, $P>0.05$; Table 3).

A preliminary mtDNA analysis (Ovenden *et al.* 1989) suggested that Tasmanian east and west coast samples might be distinguishable. However, subsequent and more detailed examinations failed to support this suggestion (Smolenski *et al.* 1993). Analysis of composite haplotypes across samples, whether using six-base cutting restriction enzymes or four-base cutters, produced G_{ST} values of ~6%, no greater than expected from chance (Table 4). The four-base enzyme analysis was really too sensitive; each composite haplotype was only seen once. However, if the analysis is restricted to each of the three four-base cutters separately, and then to those morphs seen more than once, then there is significant heterogeneity in the data. Smolenski *et al.* (1993) suggested that there is a genetically distinct subpopulation off New South Wales, whereas South Australian and Tasmanian samples are relatively homogeneous (albeit with possible temporal variation off Kangaroo Island).

Finally, 10 microsatellite loci have been studied in samples of roughy (Oke *et al.* 1999). Preliminary analysis of these data indicates that there is heterogeneity within the SEF region, although the extent and nature of this has still to be described (C. Oke, personal communication).

There is no consistent pattern of orange roughy population differentiation. Contrary conclusions have been drawn from different data sets. Any spatial genetic population differentiation that does exist must be weak; marked differentiation should have been technique- and laboratory-independent, and readily apparent.

Blue eye trevalla

An allozyme survey of *Hyperoglyphe antarctica* (Bolch *et al.* 1993) failed to reveal population differentiation. Samples were examined from mid-New South Wales, Tasmania and

South Australia. The overall G_{ST} value was a non-significant 0.004 (Table 3). This study identified a second trevalla species, the ocean blue eye (*Schedophilus labyrinthicus*), in the New South Wales component of the fishery.

Smooth oreo

There was no significant differentiation between a single Tasmanian collection and a single West Australian collection of *Pseudocyttus maculatus* (Ward *et al.* 1998), for either allozymes (Table 3) or mtDNA (Table 4). In both cases the observed G_{ST} was less than 1% and not significantly greater than that of sampling error.

Warty oreo

Three Australian samples of *Allocyttus verrucosus* were analysed, from southern New South Wales, southern Tasmania, and Western Australia (Ward *et al.* 1998). There was evidence of genetic differentiation; the overall G_{ST} value of 0.013 (Table 3) was significantly ($P = 0.003$) greater than that expected of sampling error. This was because of differentiation at just one of the eight polymorphic allozyme loci studied, *MPI**. At this locus ~5% of the variation arose from sample differentiation ($P<0.001$), with the Tasmanian sample being significantly different from the other two samples. There was no significant mtDNA differentiation (Table 4). The provisional conclusion was that southern Tasmania is a separate subpopulation from New South Wales and Western Australia. However, this needs to be validated with additional data.

Spikey oreo

Allozyme analysis of *Neocyttus rhomboidalis* (Elliott *et al.* 1998) gave a high and significant value for G_{ST} (0.074, $P<0.001$; Table 3). Closer examination of the data shows that this was almost entirely due to the locus *sSOD**. If this locus is excluded, the G_{ST} value falls to 0.008 (non-significant, $P = 0.068$). The extensive *sSOD** differentiation is not spatially related but depth related; allele frequencies of shallow (<700 m) and deep samples being consistently quite different. Minor spatial differences at two loci (*MPI** and *PGM-1**) suggested two Australian stocks: one including the GAB from South Australia to Western Australia, the other the SEF region. There was no evidence of any mtDNA differentiation (Table 4). It was suggested that the shallow–deep *sSOD** differences, given that they were not reflected in any other allozymes nor in mtDNA, were more likely to reflect natural selection than reproductive isolation.

Jack mackerel

Richardson (1982*a*) examined six polymorphic enzymes in 11 Australian samples of *Trachurus declivis*, eight from the SEF (southern New South Wales, Bass Strait, eastern Tasmania) and three from Western Australia. The overall G_{ST} value (Table 3) is ~2%, significantly greater than expected by sampling error alone ($P = 0.001$). Richardson (1982*a*) wrote that the WA samples differ significantly in frequencies at two loci, indicating that the WA samples were from a distinct subpopulation. Further, there were lesser, but significant, gene frequency differences between some eastern Australian samples. This heterogeneity, taken in association with homozygote excesses (from Hardy-Weinberg equilibrium) for some loci and samples, led him to suggest that there might be multiple stocks or subpopulations in Australian waters.

A small-scale investigation of mtDNA diversity (Smolenski *et al.* 1994) revealed barely significant heterogeneity in composite haplotypes among four SEF samples with 11 six-base restriction enzymes ($G_{ST} = 0.082$, $P = 0.045$) but not with four four-base enzymes ($G_{ST} = 0.080$, $P = 0.436$). As with the orange roughy example discussed above, the composite haplotypes from the four-base enzymes were virtually all unique, reducing the power of the analysis. Considering each four-base enzyme separately, and just those haplotypes that occur more than once, gave some evidence of significant heterogeneity (*DdeI*, P~0.001; *MboI*, P~0.035; *TaqI*, P~0.043; *MspI*, P~0.056). The 1990 eastern Tasmania sample appeared to be different from the other three samples (eastern Tasmania 1989 and two 1988 New South Wales samples). Smolenski *et al.* (1994) concluded that their data provided some support for Richardson's (1982*a*) earlier suggestion of genetically distinct schools of jack mackerel in south-eastern Australia, but further data were required to elucidate the population structure of this species.

Gummy shark

Five polymorphic allozymes in eight samples of *Mustelus antarcticus* from southern Australian waters failed to reveal any signs of population differentiation (Gardner and Ward 1998). The overall G_{ST} was a relatively high 3%, but this was completely accountable in terms of sampling error, $P = 0.468$ (Table 3). Mitochondrial DNA analysis also failed to reveal heterogeneity. These data are consistent with a single stock in these southern waters. Allozyme data (not presented here) suggest that there is a separate subpopulation off northern New South Wales (Gardner and Ward 1998).

Green back flounder

Four of seven polymorphic allozyme loci showed significant ($P<0.001$) differentiation among six SEF samples of *Rhombosolea tapirina* (van den Enden *et al.* 2000). Most of this was associated with a sample from the west coast of Tasmania (Macquarie Harbour); there was little differentiation among the four remaining northern and south-eastern Tasmanian samples, whereas a Victorian sample showed significant differentiation at one locus. The overall G_{ST} value (Table 3) is ~2%, significantly greater than expected by sampling error alone ($P<0.001$).

Venerid clam

Six polymorphic allozyme loci were used to examine the venerid clam *Katelysia scalarina* on both a medium (three Tasmanian samples) and broad scale (Tasmania, Victoria, South Australia and Western Australia) (Soh *et al.* 1998). Significant heterogeneity ($P \leq 0.005$) was observed at all loci, although G_{ST} values were low (0.008–0.053) for all but the *PGM** locus (0.298); the average was 0.086 ($P<0.001$; Table 3). There was no significant differentiation of the three geographically separated Tasmanian samples. However, these samples were clearly separated from the mainland samples (implying a Bass Strait barrier), with the Western Australian sample also showing distinction from the more eastern samples. This shallow water clam has a 10–12-day larval period; the genetic results suggest that there is gene flow, possibly via stepping-stone migration, along suitable coastlines, and that the Bass Strait provides a significant barrier to gene flow.

Abalone

Samples of the blacklip abalone (*Haliotis rubra*) from New South Wales, Victoria, Tasmania, South Australia and Western Australia have been investigated by allozyme electrophoresis (Brown 1991). Seventeen samples were examined for 15 loci. G_{ST} values for the 12 variable loci ranged from zero to 0.061, with an overall value of 0.033 ($P<0.001$; Table 3), and significant differentiation was observed at eight loci. Although geographically similar samples (e.g. five Tasmanian, six Victorian, four South Australian) genetically cluster together into regional groups, the overall conclusion was that the species had predominantly local recruitment, with the high local gene-flow governed by large local effective population sizes. The larval period is quite short at 3–11 days. The results may also fit with a stepping-stone model along suitable coastlines (or 'isolation by distance') as there was strong correlation observed between genetic and geographic distances and a large contribution from populations at the extremes of the sampling range to the significant results. However, some geographically close samples were found to be genetically distinguishable, mainly physically isolated reefs or island populations. Significant differentiation of combined Victorian samples from combined Tasmanian samples supports the likelihood of Bass Strait acting as a barrier to gene flow.

Huang *et al.* (2000) investigated the use of 84 polymorphic RAPD bands with six random primers, two minisatellites and three microsatellites to detect population structure in nine Victorian and one New South Wales sample of blacklip abalone. All three types of markers revealed significant subdivision. All three microsatellite loci showed excess homozygosity over Hardy-Weinberg expectations, although sample sizes were limited to a total of 100 animals over the 10 sites. Preliminary analysis of larger sample sizes (>60 per sample) from four Tasmanian and one Victorian site for four microsatellite loci showed limited sample differentiation, as did RFLP analysis of the mtDNA from 20 individuals from each site (N. Conod, B. Evans, J. Bartlett and N. Elliott, unpublished).

The population structure of the greenlip abalone (*Haliotis laevigata*) was also examined with 15 allozyme loci but a reduced number of samples: seven South Australian sites and one Tasmanian site, Flinders Island (Brown and Murray 1992). Significant differences in allele frequencies were observed at seven of the 13 variable loci. G_{ST} values for the variable loci ranged from zero to 0.048, with a mean of 0.014. The one Tasmanian sample was a major contributor to the heterogeneity at four loci, but there were still significant differences between the remaining South Australian samples at five loci. As for the blacklip abalone, there was a strong correlation (0.805) between genetic and geographic distance.

Rock lobsters

There are two commercial rock lobster species within the SEF region: the southern rock lobster (*Jasus edwardsii*) and the eastern rock lobster (*J. verreauxi*). The southern rock lobster, the more important commercial species, has a wide geographic distribution from New South Wales around Tasmania to Western Australia; the eastern rock lobster has a more restricted distribution, along the New South Wales and eastern Victoria coast and the north-east tip of Tasmania. Both species are also present in New Zealand waters. Rock lobsters have a long oceanic planktonic larval phase (phyllosoma) allowing for potentially extensive movement and gene flow. They do not have confined spawning areas. The larval phase of southern rock lobster is thought to be up to 23 months after a spring hatch, and 8–12 months for eastern rock lobster after a spring–summer hatch.

An allozyme study (Booth *et al.* 1990) of one of the few polymorphic allozymes in southern rock lobster, LDH, indicated heterogeneity within Australian samples with significant differences between samples from South Australia and southern Tasmania. Greater genetic variation was found in the mitochondrial genome (Ovenden and Brasher 1994). Nucleotide sequence diversity ranged from 0.44 to 0.96 in small samples of 4–16 animals. There was no significant differentiation among 11 samples from Western Australia, South Australia, Tasmania, Victoria and new South Wales.

Scallops

Significant heterogeneity of allele frequencies at 12 allozyme loci was observed among 15 collections of *Pecten fumatus* from south-eastern Australia (Woodburn 1988). The mean G_{ST} was 0.030±0.003. The greatest differences were between samples at the extremes of the sampling range. As the scallop is present within Bass Strait, there is more likelihood of gene flow within the SEF for this species than for others (such as the clam *Katelysia scalarina*) that are only in coastal embayments.

Trans-Tasman genetic studies

The Tasman Sea appears to be a significant barrier to gene flow for most species. Among fishes, the greenback flounder showed the largest trans-Tasman differentiation (van den Enden *et al.* 2000). Here, the New Zealand population was 'quite distinct', and differences between it and Australian populations were about an order of magnitude larger than among Australian populations; the cross-Tasman G_{ST} was about 0.15. Some small but significant differences have been observed for five other species: morwong (allozyme G_{ST} ~0.005, $P = 0.002$, Elliott and Ward 1994; mtDNA G_{ST} ~0.014, $P = 0.024$, Grewe *et al.* 1994); gemfish (allozyme, excluding esterase, G_{ST} ~0.009, $P<0.05$; mtDNA, no significant differences; Colgan and Paxton 1997); blue grenadier (allozyme G_{ST} ~0.006, $P<0.001$, Milton and Shaklee 1987; mtDNA, no significant differences, Smith *et al.* 1996); orange roughy (allozyme G_{ST} ~0.002, $P = 0.019$, Elliott and Ward 1992; mtDNA, some but not all comparisons have been statistically significant, Smolenski *et al.* 1993; Smith *et al.* 1996); and spikey oreo (allozyme, excluding sSOD, G_{ST} ~0.003, $P = 0.008$; mtDNA, no significant differences, Elliott *et al.* 1998). A survey of a single polymorphic allozyme and mtDNA in Australian and New Zealand school shark (Ward and Gardner 1997) showed weak evidence of population differentiation ($P = 0.040$ and a just non-significant 0.052, respectively). No significant allozyme or mtDNA differences were observed for two oreo species: the smooth and the black oreo (Ward *et al.* 1998).

There are few species of commercially fished invertebrates that are found in both Australia and New Zealand. The southern rock lobster showed differences for allozymes (Smith *et al.* 1980) but not for mtDNA (Ovenden *et al.* 1992). Eastern rock lobsters showed heterogeneity between New South Wales and New Zealand ($G_{ST} = 0.294$, $P = 0.004$; Brasher *et al.* 1992). Tasmanian and New Zealand samples of a venerid clam, *Ruditapes largillierti*, showed very little allozyme differentiation, although it is likely that the Tasmanian population arose from a recent inadvertent introduction from New Zealand (G. Maguire and R. Ward, unpublished).

Discussion

Fourteen allozyme studies of 12 fish species in southern Australian waters are listed in Table 3. All species showed sufficient allozyme variation that population structure studies could be satisfactorily carried out. The average heterozygosity per locus per species ranged from 5% to 14%, with a mean of 9.3%. This is a little higher than the 6.4% average of 57 marine fishes reviewed by Ward *et al.* (1994). The mean G_{ST} of the 14 studies was 0.031, one half of the mean value of 0.062 for marine fishes in Ward *et al.* (1994). The gemfish gave a high and clearly outlying G_{ST} value of 0.192. If the gemfish is dropped, then the mean G_{ST} of the 13 remaining studies falls to 0.019. Thus, on average, only ~2–3% of total genetic variation could be attributed to sample differentiation. Half of the studies showed no evidence of genetic population structuring.

Twelve mtDNA studies of eight fish species in southern Australian waters are listed in Table 4. The average nucleon or haplotype diversity was 0.597; the average nucleotide diversity (of eight studies and five species) was 0.54%. As for the allozymes, there was sufficient variation in each species for population structure analysis. The mean G_{ST} of the 12 studies was 0.116. Once again the gemfish gave a very high and clearly outlying G_{ST} value. This was 0.963, 11 times the next highest value (jack mackerel, 0.082). If the gemfish is dropped, then the mean G_{ST} falls to 0.039. Only the gemfish gave unequivocal evidence of population differentiation; jack mackerel gave a suggestion ($P = 0.045$) of structure in one analysis. Ten (83%) of the studies based on composite haplotype analysis showed no evidence of genetic population structuring. However, both orange roughy and jack mackerel gave evidence of structure when statistical analysis was based on single restriction enzymes rather than composite haplotypes (Smolenski *et al.* 1993, 1994).

It is clear that for most fish species, the extent of genetically detectable population structure within the SEF region is very small. Note, however, that failure to find evidence for population structuring does not mean that the null hypothesis of panmixia is correct; it simply means that it cannot be rejected by available evidence. There may still be undetected population subdivision.

The gemfish stands apart from all other species in the extent of its population differentiation. However, this was so marked, for both allozymes and mtDNA, that the taxonomic status of the two stocks might be questioned. Possibly these should be considered as subspecies, or even sibling species, although a morphological investigation carried out alongside the genetic study failed to find any discriminating characteristics (Colgan and Paxton 1997).

The invertebrate species show more evidence of population structure than the fish species. All five invertebrate species examined within southern Australian waters — a clam, two species of abalone, a scallop and a rock lobster — show significant population differentiation following allozyme analysis. The average (allozyme) G_{ST} was 0.053, about twice that of fish species. The enhanced population differentiation of the shellfish may reflect both a generally shorter larval period than fish (although that of the rock lobster is several months), reducing dispersal in early life-history stages, and a less mobile adult stage. Both these factors will reduce gene flow.

Seven of nine fish species showed significant genetic differences between Australian and New Zealand samples. Although this looks like striking confirmation that the Tasman Sea does act as a gene barrier, in fact all but one of the significant allozyme cases have G_{ST} values less than 0.01. Thus the degree of differentiation is generally very small. Only the greenback flounder has, at a high 0.15, a G_{ST} value greater than 0.01 (van den Enden *et al.* 2000). The average G_{ST} value is 0.022, dropping to only 0.004 if flounder is excluded. These G_{ST} values are no greater than those observed in inter-Australian comparisons. The enhanced cross-Tasman differentiation of the flounder may be related to its ecology; this was the only inshore coastal species examined. However, it spawns not only in deeper areas of tidal rivers and estuaries (which might be expected to enhance population differentiation), but also in offshore waters. The other fish species are all offshore species, with egg, larval and adult stages that are expected to promote gene flow and retard differentiation.

Most of the statistically significant examples of differentiation come from allozyme analysis; proportionately fewer of the mtDNA analyses showed differences (seven of nine versus two of seven studies, respectively). This is perhaps a little surprising considering that in principle, mtDNA analysis is expected to be more sensitive to population differentiation than allozyme (nuclear DNA) analysis. Because mtDNA is haploid and maternally inherited, it has a smaller effective population size than nuclear DNA; it should therefore be more responsive to genetic drift. However, the mtDNA sample sizes were generally smaller than the allozyme sample sizes, often much smaller. In many instances they would be completely inadequate to detect the low levels of differentiation expected by extrapolating from the allozyme studies. Sample sizes need to be at least 50 for a reasonable test of population differentiation; most of the mtDNA studies did not reach this level. This seems a plausible explanation for the apparent differences between the two analytical methods. Another possibility is that allozymes offer multiple independent tests of the null hypothesis (allozymes are independent markers), whereas the mtDNA genome offers only a single test; in situations where differentiation is low, several polymorphic allozymes may have more power than a single mtDNA genome.

The general low levels of genetic differentiation of marine species, including shellfish, off southern Australia and including New Zealand, are likely to reflect both passive drift of young stages in currents and adult movements. Egg and larval drift permits gene flow across areas where adults may be absent, such as the Tasman Sea. The two major currents (Fig. 1) affecting this region (Church and Craig 1998; Cresswell 2000) are (1) the warm waters of the Leeuwin Current that follow the shelf edge across the Great Australian Bight and then flow south along the western edge of the Bass Strait and down the western coast of Tasmania (where it may be known as the Zeehan Current), and (2) the southward flowing East Australian Current (EAC) that brings warm South Pacific waters along the eastern Australian coast. Its influence extends to well below the surface waters. The EAC separates from the coast near 33°S (near the eastern boundary of SEF); some flow at this point returns north, and some has been tracked as the Tasman Front across the Tasman Sea to the northern tip of New Zealand. The remainder continues south down the eastern coast of Tasmania, in a series of anticyclonic eddies that pinch off from the main current. The strongest southward flow of the EAC is in summer and extends down the eastern Tasmanian coast. There is a deeper, cooler northward flow on the shelf. The Bass Strait flow is predominantly eastward, except in summer when westward flow may occur.

The lack of major oceanographic and environmental barriers to gene flow, together with the two major current systems, lead to the limited genetic population differentiation of most of the commercial species in the southern Australian region. However, genetic stock structuring is evident for several species of fish and shellfish, and is more marked for the coastal species (e.g. flounder, clams, abalone) than for the shelf and slope inhabiting species that constitute the bulk of species examined to date. For some of the coastal species, the isolation-by-distance model fits some of the evidence, with samples further apart showing greater differentiation from each other, and for some of these species, there is evidence for restricted gene flow across Bass Strait.

Because genetic differentiation among marine populations is both expected and observed to be low, it can become difficult to discriminate true signal from the genetic noise associated with limited sampling. These issues are dealt with by Waples (1998), who recommends sample replication over time to discern signal from noise. The low degree of differentiation for most species means that sample sizes should be at least 50 and preferably 100 or more to get reasonable statistical power. It also means that investigators have to be careful in deriving conclusions; small differences between samples may arise from experimental error rather than true differences. Consistency between independent samples from the same spatial area would support the conclusion of small but real differences; lack of consistency, as often seen here in independent studies of the same species, may more likely point to sampling error of some kind than true micro-scale spatial heterogeneity. More comprehensive genetic studies of species in the SEF region are required. These should have an increased scale of temporal and spatial sampling, and should deploy a wider range of markers. The marine biosphere is being increasingly exploited for food; sustainable management is essential for any continued harvesting, and this in turn requires good knowledge of population structure. Although genetic approaches are not the only means of investigating such issues, they provide information of fundamental importance and will continue to be applied.

Acknowledgments

We are grateful to Adam Smolenski and Sharon Appleyard for commenting on a draft of this paper.

References

Black, M., and Dixon, P. I. (1989). Population structure of orange roughy (*Hoplostethus atlanticus*) in Australian waters. Unpublished report. (Centre for Marine Science, University of New South Wales: Australia.)

Bolch, C. J. S., Elliott, N. G., and Ward, R. D. (1993). Enzyme variation in south-eastern Australian populations of the blue-eye or deepsea trevalla, *Hyperoglyphe antarctica* Carmichael 1818 (Teleostei : Stromateoidei). *Australian Journal of Marine and Freshwater Research* **44**, 687–97.

Booth, J. D., Street, R. J., and Smith P. J. (1990). Systematic status of the rock lobsters *Jasus edwardsii* from New Zealand and *J. novaehollandiae* from Australia. *New Zealand Journal of Marine and Freshwater Research* **24**, 239–49.

Brasher, D. J., Ovenden, J. R., Booth, J. D., and White, R. W. G. (1992). Genetic subdivision of Australian and New Zealand populations of *Jasus verreauxi* (Decapoda : Palinuridae) – preliminary evidence from the mitochondrial genome. *New Zealand Journal of Marine and Freshwater Research* **26**, 53–8.

Brown, L. D. (1991). Genetic variation and population structure in the blacklip abalone, *Haliotis rubra*. *Australian Journal of Marine and Freshwater Research* **42**, 77–90.

Brown, L. D., and Murray, N. D. (1992). Population genetics, gene flow, and stock structure in *Haliotis rubra* and *Haliotis laevigata*. In 'Abalone of the World, Biology, Fisheries and Culture'. (Eds S. A. Shepherd, M. J. Tegner and S. A. Guzman del Proo.) pp. 24–33. (Fishing News Books, Blackwell Scientific: Oxford.)

Carvalho, G. R., and Hauser, L. (1994). Molecular genetics and the stock concept in fisheries. *Reviews of Fish Biology and Fisheries* **4**, 326–50.

Church, J. A., and Craig, P. D. (1998). Australia's shelf seas: diversity and complexity. Coastal segment (30, W-S). In 'The Sea'. (Eds A. R. Robinson and K. H. Brink.) Vol. 11, pp. 933–64. (John Wiley: Chichester.)

Colgan, D. J., and Paxton, J. R. (1997). Biochemical genetics and recognition of a western stock of the common gemfish, *Rexea solandri* (Scombroidea : Gempylidae), in Australia. *Marine and Freshwater Research* **48**, 103–18.

Cresswell, G. (2000). Currents of the continental shelf and slope of Tasmania. *Proceedings of the Royal Society of Tasmania* **133**, 21–30.

Daley, R., Last, P., Yearsley, G., and Ward, R. (1997). 'South East Fishery Quota Species: an Identification Guide.' (CSIRO Marine Research: Australia.)

Deriso R., and Quinn, T. (co-chairs) (1998). 'Improving Fish Stock Assessments.' (National Academy Press: Washington, DC.)

Elliott, N. G., and Ward, R. D. (1992). Enzyme variation in orange roughy, *Hoplostethus atlanticus* (Teleostei : Trachichthyidae), from southern Australian and New Zealand waters. *Australian Journal of Marine and Freshwater Research* **43**, 1561–71.

Elliott, N. G., and Ward, R. D. (1994). Enzyme variation in jackass morwong, *Nemadactylus macropterus* (Schneider, 1801) (Teleostei : Cheilodactylidae), from Australian and New Zealand waters. *Australian Journal of Marine and Freshwater Research* **45**, 51–67.

Elliott, N. G., Lowry, P. S., Grewe, P. M., Innes, B. H., Yearsley, G. K., and Ward, R. D. (1998). Genetic evidence for depth- and spatially-separated stocks of the deepwater spikey oreo in Australasian waters. *Journal of Fish Biology* **52**, 796–816.

Gardner, M. G., and Ward, R. D. (1998). Population structure of the Australian gummy shark (*Mustelus antarcticus* Günther) inferred from allozymes, mitochondrial DNA and vertebrae counts. *Marine and Freshwater Research* **49**, 733–45.

Grant, W. S., García-Marín, J. L., and Utter, F. M. (1999). Defining boundaries for fishery management. In 'Genetics in Sustainable Fisheries Management'. (Ed. S. Mustafa.) pp. 27–72. (Fishing News Books, Blackwell Scientific: Oxford.)

Grewe, P. M., Smolenski, A. J., and Ward, R. D. (1994). Mitochondrial DNA diversity in jackass morwong (*Nemadactylus macropterus*: Teleostei) from Australian and New Zealand waters. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1101–9.

Huang, B. X., Peakall, R., and Hanna, P. J. (2000). Analysis of population genetics structure of blacklip abalone (*Haliotis rubra*) using RAPD, minisatellite and microsatellite markers. *Marine Biology* **136**, 207–16.

Milton, D. A., and Shaklee, J. B. (1987). Biochemical genetics and population structure of blue grenadier, *Macruronus novaezelandiae* (Hector) (Pisces : Merluccidae), from Australian waters. *Australian Journal of Marine and Freshwater Research* **38**, 727–42.

Nei, M. (1973). Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Science, USA* **70**, 3321–3.

O'Connell, M., and Wright, J. M. (1997). Microsatellite DNA in fishes. *Reviews in Fish Biology and Fisheries* **7**, 331–63.

Oke, C. S., Ching Crozier, Y., Crozier, R. H., and Ward, R. D. (1999). Microsatellites from a teleost, orange roughy (*Hoplostethus atlanticus*), and their potential for determining population structure. *Molecular Ecology* **8**, 2145–7.

Ovenden, J. R., and Brasher, D. J. (1994). Stock identity of the red (*Jasus edwardsii*) and green (*J. verreauxi*) rock lobsters inferred from mitochondrial DNA analysis. In ' Spiny Lobster Management'. (Eds B. F. Phillips, J. S. Cobb and J. Kittaka.) pp. 230–49. (Blackwell Scientific: Oxford.)

Ovenden, J. R., Brasher, D. J., and White, R. W. G. (1992). Mitochondrial DNA analysis of the red rock lobster *Jasus edwardsii* supports an apparent absence of population subdivision throughout Australia. *Marine Biology* **112**, 319–26.

Ovenden, J. R., Smolenski, A. J., and White, R. W. G. (1989). Mitochondrial DNA restriction site variation in Tasmanian populations of orange roughy (*Hoplostethus atlanticus*), a deep water marine teleost. *Australian Journal of Marine and Freshwater Research* **40**, 1–9.

Park, L. K., and Moran, P. (1994). Developments in molecular genetic techniques in fisheries. *Reviews in Fish Biology and Fisheries* **4**, 272–99.

Richardson, B. J. (1982*a*). Geographical distribution of electrophoretically detected protein variation in Australian commercial fishes. II. Jack mackerel, *Trachurus declivis* Jenyns. *Australian Journal of Marine and Freshwater Research* **33**, 917–26.

Richardson, B. J. (1982*b*). Geographical distribution of electrophoretically detected protein variation in Australian commercial fishes. II. Jackass morwong, *Cheilodactylus macropterus* Bloch and Schneider. *Australian Journal of Marine and Freshwater Research* **33**, 927–31.

Smith, P. J., McKoy, J. L., and Machin, P. J. (1980). Genetic variation in the rock lobster *Jasus edwardsii* and *Jasus novaehollandiae*. *New Zealand Journal of Marine and Freshwater Research* **14**, 55–63.

Smith, P. J., McVeagh, S. M., and Ede, E. (1996). Genetically isolated stocks of orange roughy (*Hoplostethus atlanticus*), but not of hoki (*Macruronus novaezelandiae*), in the Tasman Sea and southwest Pacific Ocean around New Zealand. *Marine Biology* **125**, 783–93.

Smolenski, A. J., Ovenden, J. R., and White R. W. G. (1993). Evidence of stock separation in southern hemisphere orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) from restriction-enzyme analysis of mitochondrial DNA. *Marine Biology* **116**, 219–30.

Smolenski, A. J., Ovenden, J. R., and White R. W. G. (1994). Preliminary investigation of mitochondrial DNA variation in jack mackerel (*Trachurus declivis*, Carangidae) from south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **45**, 495–505.

Soh, S. W. L., Maguire, G. B., and Ward, R. D. (1998). Genetic studies of the venerid clam genus *Katelysia*. *Journal of Shellfish Research* **17**, 1057–64

van den Enden, T., White, R. W. G., and Elliott, N. G. (2000). Genetic variation in the greenback flounder *Rhombosolea tapirina* Günther (Teleostei, Pleuronectidae) and the implications for aquaculture. *Marine and Freshwater Research* **51**, 23–33.

Waples, R. S. (1998). Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity* **98**, 438–50.

Ward, R. D. (2000). Genetics and fisheries management. *Hydrobiologia* **420**, 191–200.

Ward, R. D., and Gardner, M. G. (1997). Stock structure and species identification of school and gummy sharks in Australasian waters. Final Report Project 93/64 (Fisheries Research and Development Corporation: Canberra.)

Ward, R. D., and Grewe, P. M. (1994). Appraisal of molecular genetic techniques in fisheries. *Reviews in Fish Biology and Fisheries* **4**, 300–25.

Ward, R.D., and Reilly, A. (2001). Development of microsatellite loci for population studies of the pink ling, *Genypterus blacodes* (Teleostei: Ophidiidae). *Molecular Ecology Notes*, in press.

Ward, R. D., Skibinski, D. O. F., and Woodwark, M. (1992). Protein heterozygosity, protein structure and taxonomic differentiation. *Evolutionary Biology* **26**, 73–159.

Ward, R. D., Woodwark, M., and Skibinski, D. O. F. (1994). A comparison of genetic diversity levels in marine, freshwater and anadromous fish. *Journal of Fish Biology* **44**, 213–32.

Ward, R. D., Elliott, N. G., Grewe, P. M., Last, P. R, Lowry, P. S., Innes, B. H., and Yearsley, G. K. (1998). Allozyme and mitochondrial DNA variation in three species of oreos (Teleostei : Oreosomatidae) from Australasian waters. *New Zealand Journal of Marine and Freshwater Research* **32**, 233–45.

Ward, R. D., Appleyard, S. A., Daley, R. K., and Reilly, A. (2001). Population structure of pink ling (*Genypterus blacodes*) from south-eastern Australian waters, inferred from allozyme and microsatellite analyses. *Marine and Freshwater Research* **52** (in press).

Woodburn, L. (1988). Genetic variation in southern Australasian *Pecten*. In 'Proceedings of the Australasian Scallop Workshop'. (Eds M. L. C. Dredge, W. F. Zacharin and L. M. Joll.) pp. 226–40, (Tasmanian Government Printer: Hobart, Australia.)

Yearsley, G., Last, P., and Ward, R. D. (1999). 'Handbook of Australian Seafood Vol. I. Domestic Species.' (CSIRO Marine Research: Hobart, Australia.)

Manuscript received 16 December 1999; revised and accepted 3 April 2000

Mar. Freshwater Res., 2001, **52**, 575–87

Reproductive characteristics and per-recruit analyses of blue warehou (*Seriolella brama*): implications for the South East Fishery of Australia

Ian A. Knuckey and K. P. Sivakumaran

Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Vic. 3225, Australia

Abstract. Monthly samples of commercial catches of *S. brama* were collected between May 1996 and December 1997 in three regions of the fishery: off the east coast of Victoria; eastern Tasmania; and western Bass Strait. Sex ratio, gonadosomatic index, macroscopic and histological development, size at maturity and fecundity were estimated and combined with data on growth and mortality to perform per-recruit analyses. The main spawning period was during winter–spring and there was evidence of spawning in each of the three regions. Blue warehou reach maturity at 30–40 cm fork length. They have a determinate annual fecundity and spawn around three batches of eggs during a season. Eggs-per-recruit analyses revealed maximum egg production at ~40 cm (4–5 years) in an unfished population. Gill-net fishing, which targets fish >45 cm, was less likely to affect the relative eggs-per-recruit in a population than trawl fishing, which catches a wider range of smaller fish. These results are discussed in light of the current management arrangements in the fishery and will be used in models to assess the effect of fishing on the long-term sustainability of blue warehou.

Extra keywords: reproduction, spawning, fecundity, eggs-per-recruit.

Introduction

Blue warehou, *Seriolella brama* (Centrolophidae), is an important component of the South East Fishery (SEF), sold predominantly as fresh fish in the Sydney and Melbourne fish markets. Trawled blue warehou catches come mainly from outer-shelf and upper-slope waters off southern New South Wales, eastern Bass Strait and western Victoria, and significant gill-net catches were previously caught from shelf waters in eastern Bass Strait and around inshore Tasmanian waters (Smith 1994). Blue warehou is also an increasingly important recreational target species in coastal waters of Victoria, Tasmania and southern New South Wales.

Historical catch records often failed to distinguish blue warehou from the closely related silver warehou (*S. punctata*), grouping them together as warehou or 'Tassie trevally'. Catches of warehou increased dramatically during the 1980s and total landings of the two species in the early 1990s were >4000 t year^{-1}, with an annual landed value of ~$A10 million. The combined catch of these species has since stabilized around this tonnage, but the proportion (by weight) of the more valuable blue warehou dropped from ~70% to 40% during the mid 1990s. In 1997, the total blue warehou catch had fallen to ~1000 t with a value of $A1.5 million (Smith *et al.* 1998).

In conjunction with declining catches, blue warehou catch rates in both the trawl and non-trawl sectors declined during the mid 1990s. This decline was accompanied by significant reduction in the mean catch-at-age in some sectors of the fishery which led to concerns over the status of blue warehou stocks in the 1994 and 1995 stock assessments (Smith 1995; MacDonald and Smith 1996). Such concerns were compounded by a poor understanding of blue warehou population dynamics and the complex spatial and temporal fluctuations in their distribution (Smith *et al.* 1998), which prevented assessment of the relative importance of fishing pressure *versus* other factors in producing these trends. Consequently, the South East Fishery Assessment Group recommended a study on blue warehou reproductive biology to help develop an age-structured model of the different sectors of the fishery (Staples and Tilzey 1994).

Previous studies on the reproductive biology of warehou in New Zealand (Gavrilov 1976) and Australian (Smith *et al.* 1995) waters were very preliminary. This paper presents the results of a comprehensive study to describe gonad development and spatial and temporal patterns in the reproductive cycle and provide reproductive parameters, including size/age at maturity, gonadosomatic index (GSI), annual fecundity and batch fecundity. This information was combined with previously unpublished data on growth and mortality to conduct per-recruit analyses of the effect of different intensities of fishing pressure on egg production and yield in the trawl and gill-net fisheries. The effect of the use of particular fishing methods on spawning stocks is discussed. Such information will be used in stock assessment models and evaluation of harvest strategies

10.1071/MF00022 1323-1650/01/040575

designed to optimize reproductive capacity and recruitment of blue warehou in south-eastern Australian waters.

Materials and methods

Sampling regime

The study was undertaken in the upper-shelf and mid-slope waters of three main fishing regions in the SEF: off Eden to Lakes Entrance (East); eastern Tasmania; and off Portland in western Bass Strait (West) (Fig. 1). Preliminary sampling began in May 1996 to determine the most suitable sampling methods, preservation techniques and gonad-staging classifications. From January to December 1997, random samples of >100 blue warehou were collected from commercial trawl (90 mm codend stretched) and gill-net (150 mm monofilament) catches in the three regions. Logbook data from commercial trawl (SEF1) and gill-net (GN01) sectors of the SEF during 1986 to 1997 were used to determine the timing of the fisheries in the three regions.

Selectivity of trawls and gill-nets to blue warehou were derived from Punt (1999) except that the left-hand side of the trawl selectivity ogive was estimated from back-calculation of total mortality from length-converted catch-curve analysis (e.g. Jensen 1982; Pauly 1984) on length–frequency distributions obtained from on-board observer measurements of trawl catches.

Biological data

After capture, all fish samples were retained on ice and returned to the laboratory for dissection. The sex (male, female or immature), length to caudal fork measured to the nearest centimetre (LCF) and total weight (± 50 g) were recorded for each fish. The weight of the left and right gonad was recorded (± 0.5 g), and GSI was determined

$$\mathrm{GSI} = \frac{\text{Gonad weight}}{\text{Total weight}} \times 100$$

Macroscopic gonad stages (Tables 1 and 2) were based on similar reproductive studies (e.g. West 1990), particularly one on another centrolophid, the blue-eye trevalla, *Hyperoglyphe antarctica* (Baelde 1996).

During 1996, gonads were fixed and preserved in vapour-suppressed 4% formaldehyde fixative. Although this technique was sufficient for most samples, it proved inadequate for histological examination of female Stage VI gonads because the samples were not firm enough to allow sectioning. As a consequence, fecundity was not estimated from samples collected during 1996, and a modified technique was established for sampling during 1997. This involved preservation of the entire gonad in 10% formalin in seawater for a week before a transverse medial portion of about 30 g of gonad was removed and preserved in Davidson's solution. In the case of ripe female gonads (Stage V and VI), the whole left or right ovary was preserved in Davidson's solution.

Histological analysis

In many studies, no significant differences in oocyte frequency distribution and maturation have been found between right and left ovaries (DeMartini and Fountain 1981; West 1990). In the present study, we usually removed a portion from the left-hand ovary unless it was damaged. To avoid possible variation in the developmental stage of oocytes due to their position in the ovary, only a transverse medial portion of the gonad was removed from each sample for histological examination (e.g. Forberg 1982; Gooley *et al.* 1995). The subsamples were embedded in paraffin wax and 6 µm sections were cut, mounted and stained in Harris' haematoxylin and eosin (Luna 1968).

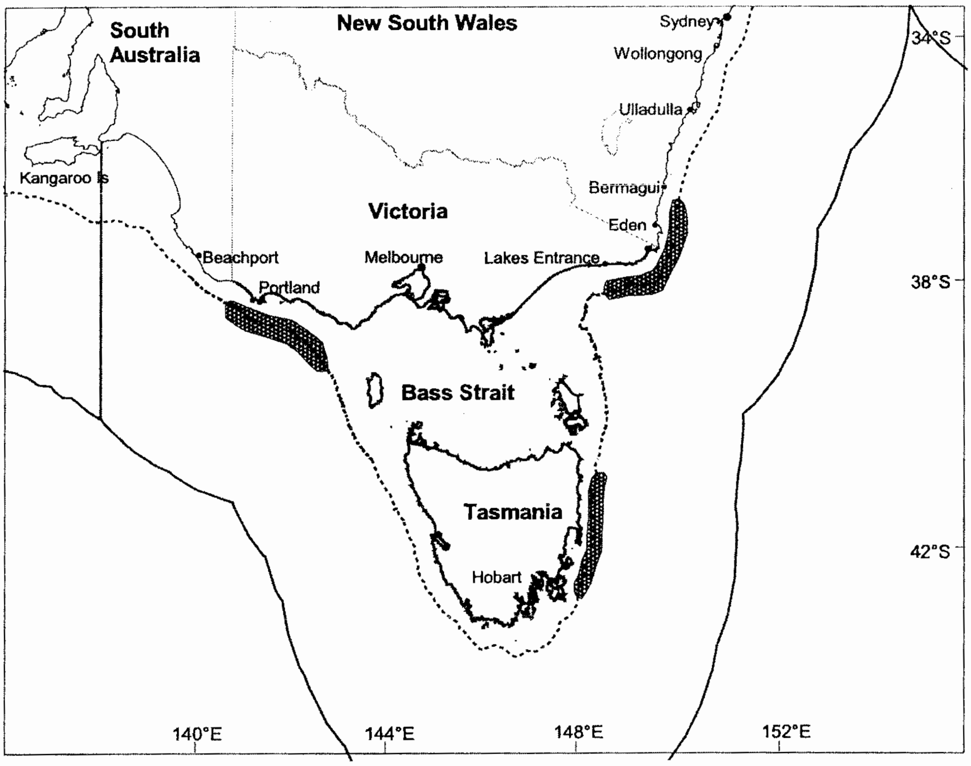


Fig. 1. Blue warehou were sampled from upper-shelf and mid-slope waters within three regions (shaded) of the South East Fishery: off Eden to Lakes Entrance (East); Eastern Tasmania; and off Portland in western Bass Strait (West).

Table 1. Macroscopic description of the developmental stages and of the gonads of male blue warehou

Stage		Macroscopic description
I	Immature	Testes very small, flat, and thread-like
II	Early developing	Testes flat/rounder in shape Testes occupy 20–70% of length of body cavity
III	Developing	Testes lobed Marked groove in the middle of each testis Testes occupy 40–70% of length of body cavity Creamy or white milt sometimes present
IV	Late developing /Running-ripe	Testes very large and lobed/multilobed Testes occupy 40–70% of length of body cavity Free-flowing milt Testes white or pinkish, sometimes bloodshot
V	Spent & Resting	Testes very bloodshot Testes occupy 20–50% of length of body cavity Milt sometimes present Testes brownish and rubbery as they regress to resting stage

The histological sections were used to describe the different stages of oocyte development (Table 2). Images of the various stages are shown in Fig. 2. The presence of postovulatory follicles, migratory-nucleus oocytes or hydrated oocytes in ovaries was used to identify individuals that had begun to spawn (Hunter and Macewicz 1985*b*) or were capable of spawning (Bell *et al.* 1992). After spawning, residual oocytes and unwanted material are reabsorbed in a process known as atresia (Hunter and Macewicz 1985*a*; Marshall *et al.* 1993). Atretic oocytes were recognized by their irregular shape, breakdown in fine structure (disintegration of the nucleus and liquefaction of yolk granules) and hypertrophy of the granulosa cells (Davis 1977). As degeneration progresses, it becomes more difficult to distinguish atretic oocytes from advanced degeneration of postovulatory follicles (described as beta atresia by Hunter and Macewicz 1985*b*). Nevertheless, high levels of any atretic material, combined with the lack of hydrated oocytes and postovulatory follicles, were used to confirm when spawning had ceased.

Fecundity

Even though fish may spawn repeatedly during a season, if a stock of yolked oocytes destined to be spawned in a season is identifiable from the unyolked oocytes at the beginning of the spawning season, annual fecundity may be considered to be determinate (Yamamoto 1956; Hunter and Macewicz 1985*a*, 1985*b*). To establish this for blue warehou, sections from representative Stage II to Stage VI ovaries were selected and all individual oocytes were staged and then measured by taking the mean of the maximum and minimum diameter of all oocytes that had been sectioned through the nucleus. The size frequency of the unyolked, yolked and hydrated oocytes was then plotted for each gonad stage.

All fecundity estimates were based on fish that had undamaged ovaries and showed no sign of previous spawning in that season (i.e. no loose, hydrated oocytes in the lumen of the ovary, Watson *et al.* 1992), no sign of postovulatory follicles and no sign of major atresia. Initially, 1 g portions from five of these fish were dissected from the anterior, median and posterior regions of the gonad and weighed accurately (±0.001 g). Analysis of variance (ANOVA) was used to compare the number of oocytes per gram between fish, and between subsamples across the ovary (near the periphery and near the centre) and along the ovaries (in the anterior, median, and posterior regions). Because no significant differences ($P > 0.05$) were observed between fish, between subsamples across the ovaries, or between subsamples along the ovaries, the medial gonad portions were weighed accurately and used to estimate fecundity by the gravimetric method (Hunter *et al.* 1985). The average relative fecundity was measured as the number of oocytes per gram (gutted weight).

Annual fecundity was estimated from the standing stock of yolked oocytes (Stage IV and V) from samples collected during 1997 spawning season. Batch fecundity, where fish may spawn more than one batch of eggs within a spawning season, was estimated from counts of hydrated oocytes in the nine suitable Stage VI ovaries.

Size at maturity

It was difficult to distinguish, either macroscopically or histologically, between immature developing males and mature males with gonads that were redeveloping after spawning. Because of this, a maturity ogive was not developed for males.

Females with ribbon-like ovaries (Stage I or Stage IIa) were classed as immature. Females with ova redeveloping after spawning (Stage IIb) were more likely to have a thick flaccid gonad wall and could be recognized histologically by postovulatory follicles and/or atretic material around the oocytes. These were classed as mature fish. Some females with Stage II gonads and all females with Stage III gonads could not be classified as mature or immature and were not included in size-at-maturity estimates. Size at maturity was established by counting the number of mature fish within each 1 cm length-class as a percentage of the total number of fish of that length-class. A logistic curve was fitted to data (pooled across areas) by the use of a non-linear least-squares procedure weighted by the number of fish in each length-class. The form of the logistic equation used was

$$\% \text{ mature} = 100 / (1 + e^{a\,(b - c)}),$$

where a is the rate of increase in maturity, b is length at 50% maturity (L_{m50}) and c is the 1 cm length-class.

Per-recruit analyses

Per-recruit modelling involved use of a Microsoft Excel spreadsheet (Sanders 1995). Typical age-based models were used for yield-per-recruit (Thompson and Bell 1934; Ricker 1945; Beverton and Holt 1957) and eggs-per-recruit (remaining in the population) was calculated by including the fecundity relationship established in the present study. Both yield-per-recruit and eggs-per-recruit were modelled against age and length. Length-classes at intervals of 1 cm and of 0.25 years (determined from the inverse von Bertalanffy equation) were used to model the recruit over a period of ten years. Comparisons were made between the gill-net fishery in the East and the trawl fishery.

Based on the work by the Central Ageing Facility (Morison *et al.* 1998) at the Marine and Freshwater Resources Institute, growth parameters have been published for blue warehou (Smith 1994, 1999; Smith and Wayte 2000), but they do not distinguish between sex. For the present study, female growth was analysed separately and, based on ageing of whole otoliths, the following von Bertalanffy (1938) growth parameters were estimated: L_∞ 55.14 cm; K 0.28 year^{-1} and t_0 – 0.07 years (Morison, unpublished). The female length–weight relationship used (Knuckey, unpublished) was $w = 7.86 \times 10^{-6} \times L^{3.26}$.

Table 2. Macroscopic and histological descriptions of the developmental stages of the gonads of female blue warehou

Stage		Macroscopic description	Histological description
I	Immature	Small thread-like ovaries Ovaries pink and translucent	Chromatin nucleolar stage: very small oocytes, nucleus surrounded by a thin layer of dark-blue-stained cytoplasm
II	Early developing	Oocytes not visible Ovaries pink and translucent	Perinucleolar stage: oocyte size increases slightly as dark-blue-stained cytoplasm thickens, nucleoli appear at periphery of nucleus
IIa	First-time Developing	Ovary wall thin and transparent	
IIb	Redeveloping	Ovaries flaccid, ovary wall thick Ovary pink/greyish to yellow-orange, and opaque	
III	Developing	Small oocytes becoming visible, still translucent Ovaries sometimes change from pink to yellow-orange Ovaries occupy 20–70% of length of body cavity	Cortical alveoli stage: appearance of cortical alveoli in pale-blue-stained cytoplasm, pink-stained zona radiata distinguishable, oil vesicles appearing, lampbrush chromosomes often visible in the nucleus
IV	Late Developing(yolked)	Small opaque oocytes clearly visible Ovary wall thin and transparent Ovaries occupy 20–100% of length of body cavity	Yolk stage: marked increase in oocyte size, cytoplasm filled with pink-stained yolk granules, cortical alveoli and oil vesicles increase in size and number; degenerating postovulatory follicles visible if spawning has started
V	Ripe	Large transparent (hydrating) oocytes visible among Ovaries occupy 70–100% of length of body cavity	Nuclear migration stage: migration of nucleus to periphery of oocyte, fusion of yolk granules into yolk plates; fusion of oil vesicles into the oil droplet; degenerating postovulatory follicles visible if spawning has started
VI	Running-ripe	Hydrated oocytes very large, almost totally translucent with oil droplet visible; easily expressed from ovaries Ovaries occupy 70–100% of length of body cavity	Hydration stage: further increase in size of oocytes, all yolk granules fused into a few plates
VII	Spent & Resting	Some residual oocytes visible within translucent material Ovaries flaccid, greyish ovary wall thickened and wrinkled Ovaries occupy 20–70% of length of body cavity	Postovulatory follicles clearly visible, no yolked oocytes left except for a few undergoing atresia; structure of ovaries generally loosse, hydrated oocytes may be present in lumen

Natural mortality (M) was applied from age zero and was assumed to be constant over time; although this was a simplistic approach, no information on age-specific natural mortality rates was available. Four methods, based on life-history parameters, were used to estimate natural mortality: Beverton and Holt (1957), Hoenig (1983), Rikhter and Efanov (1976) and Pauly (1980). For Hoenig's method a lifespan of 10 years was assumed to be reached by 5% of the population (Smith and Wayte 2000). A water temperature of 10°C was assumed for Pauly's method. Fishing mortality (F) was assumed to be constant across all ages and lengths and was applied in proportion to the selectivity of the gear.

Results

Fishery data

In the East, mean monthly catches in the trawl fishery (Fig. 3) were generally below 20 t, but increased to a peak of 60–80 t in August–October before rapidly decreasing to <20 t in November. Over the longer term, there was no obvious seasonal pattern in the gill-net catches, although in 1997, when the sampling was undertaken, there was a peak in monthly catches around June, with minimal catches (<5 t) from August to December. Off eastern Tasmania, the blue warehou fishery was essentially restricted to summer (November–March), with minimal catches during the rest of the year. In contrast, the catch by trawl fishery in the West was negligible during summer, with the mean monthly catch increasing to 40–60 t during winter and spring.

In total, 3300 specimens were collected from the three areas (Table 3). Although we endeavoured to collect monthly samples of fish from both the trawl and gill-net sectors in the East region, there were no gill-net catches of blue warehou after July 1997 and samples were derived solely from trawl catches.

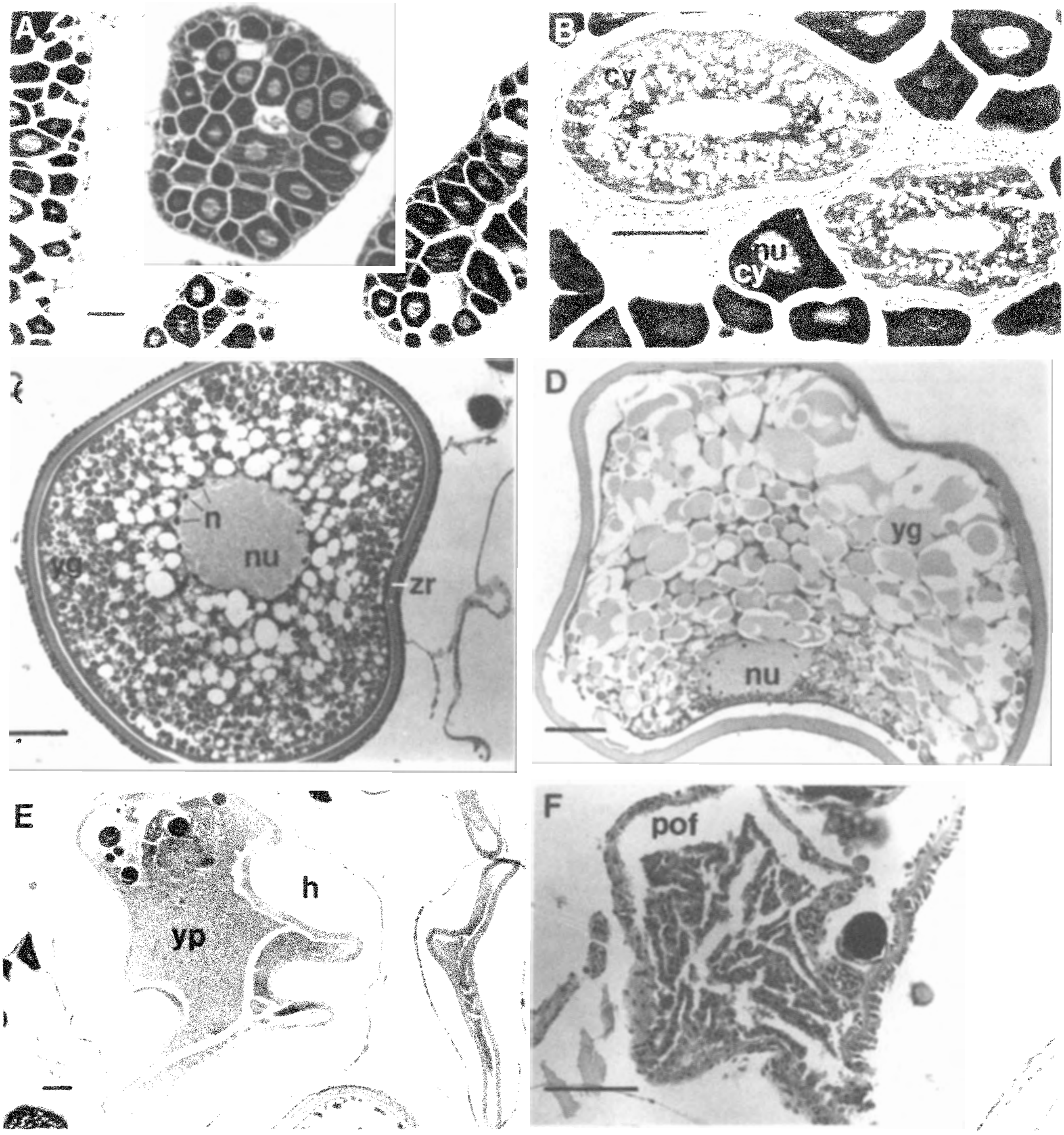


Fig. 2. Histological sections showing the maturation of blue warehou oocytes from Stage II to Stage VII (Scale bar, 50 μm). *(A, B)* Early stages: nucleoli appear at periphery of nucleus (nu); cortical alveoli apparent in cytoplasm (cy). *(C)* Stage IV: marked increase in oocyte size; nucleoli (n); cytoplasm, bounded by the zona radiata (zr), is filled with yolk granules (yg), cortical alveoli and oil vesicles. *(D)* Stage V: nucleus migrates to periphery of oocyte; yolk granules begin to fuse into yolk plates. *(E)* Stage VI: onset of hydration (h) causing cells to collapse during histological processing; yolk granules fused into a few yolk plates (yp). *(F)* After spawning: postovulatory follicles (pof).

There were noticeable differences in the size range of fish caught by the different gears and in the different regions (Fig. 4). The size of blue warehou caught by trawlers in the East ranged between 25 and 55 cm, but most were distributed between 35 and 50 cm. The gill-net catches in the East, however, generally consisted of larger fish

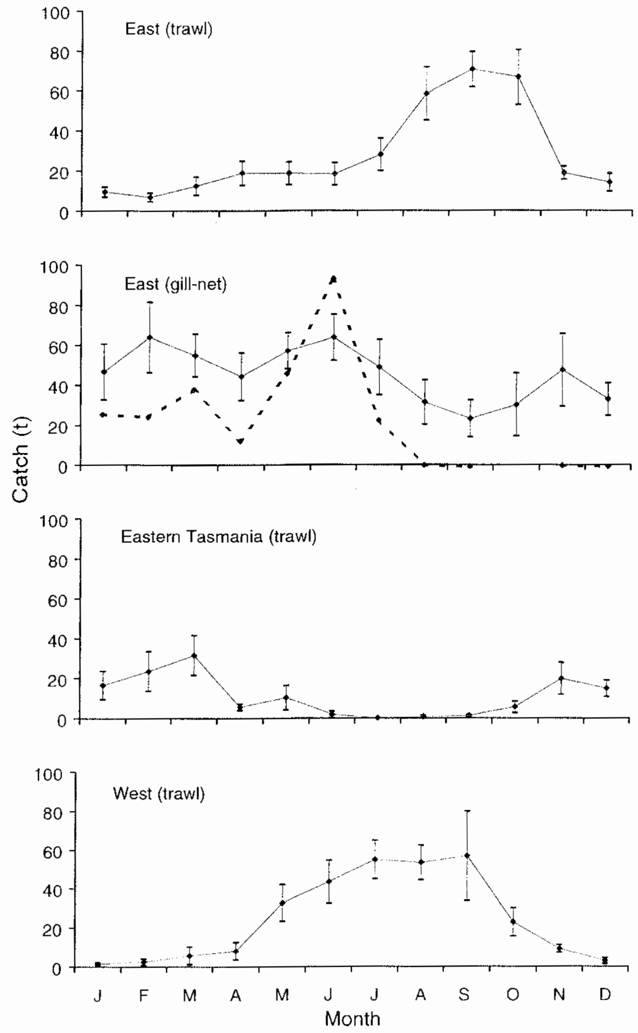


Fig. 3. Monthly catch (t, mean ± s.e.) of blue warehou landed by SEF trawl and gill-net vessels in the three regions. Trawl data were based on SEF1 logbook data 1986–97; gill-net data were based on Victorian catch-and-effort logbooks for 1986–96 and Commonwealth GN01 logbooks for 1997 and 1998. The monthly gill-net catch during the 1997 sampling period is indicated by a dashed line.

between 45 and 55 cm, with a mode around 48–49 cm. In contrast, length of trawl-caught fish in the West region generally ranged between 30 and 45 cm with a mode around 37 cm. Only 60 specimens of indeterminate sex were collected, which ranged in size between 21 and 25 cm. Generally, the size range of males and females was similar, although a greater proportion of the fish >40 cm were female.

Actual selectivity ogives for blue warehou caught by trawl and gill-net methods have not yet been established experimentally. On the basis of data derived from a stock assessment of blue warehou using integrated analysis (Punt 1999), the gill-net selectivity can be represented as

$$\% \text{ retained} = 100 / (1 + e^{0.422\,(49.64 - L)}).$$

This selectivity was based on the larger blue warehou targeted by gill-net methods in eastern Bass Strait during the 1990s and therefore also incorporates the availability of fish to that method.

The decreased selectivity of trawl gear to larger blue warehou (the right-hand side of the trawl selectivity ogive) was derived from Punt (1999) and also reflected the availability of fish to that method. This was represented by

$$\% \text{ retained} = 100 - 100 / (1 + e^{0.745\,(55.65 - L)}),$$

which was applied to fish >45 cm. Based on length–frequency distributions derived from extensive on-board monitoring of trawler catches (Knuckey and Sporcic 1999), the regression of the length-converted catch curve was $\ln(n/\mathrm{d}t) = (1.534t + 15.916$ ($R^2 = 0.97$, $P < 0.0001$), where n is the number of fish caught at age t, from which the logistic curve for the left-hand side of the trawl selectivity ogive was determined as

$$\% \text{ retained} = 100 / (1 + e^{1.570\,(34.56 - L)}).$$

The resultant selectivity ogives used for the two methods are shown in Fig. 5. Overall, the selectivity of the gill-nets was towards a smaller range of larger fish than trawl gear.

The percentage of females (30–50 cm LCF) in the monthly samples of blue warehou ranged between 50% and 75% but was usually ~60% (Fig. 6). The proportion of females increased slightly for fish >50 cm, but the total number of samples above this size was small (<100 fish). Overall, there were significantly more females caught than males ($\chi^2 = 133.57$, $P < 0.0001$).

Histological analysis

Histological slides from 522 ovaries were analysed. Of these, 39% were in spawning condition (Stage V and VI) and 1% were spent (Stage VII). Of the other 60%, 35% were yolked (Stage IV) and 65% were unyolked (Stages I to III). A monthly breakdown of the ovary conditions in the three regions is provided (Fig. 7). In the East, females with developing ova were apparent throughout the year, but the main occurrence of spawning and spent females was during May–August. A similar trend was apparent in the West, although there was no evidence of spawning until June. In both these regions, some spawning and spent females were evident until November, although there was one month in which no spawning fish were apparent (September in the East and August in the West). Data from eastern Tasmania were sparse and inconclusive, but also suggested that spawning occurred in May. These data suggest that blue warehou are likely to be group-synchronous spawners.

The development of oocytes is described in Table 2 and size frequencies of the oocytes in different stages of ovarian development are provided in Fig. 8. The average GSI and

Table 3. Monthly sample numbers from the east coast, east Tasmania and West zone of male, female and immature blue warehou collected for examination of gonad condition

Month	East Coast				East Tasmania				Western Zone				Total
	Male	Female	Immature	Total	Male	Female	Immature	Total	Male	Female	Immature	Total	
May-96	0	0	0	0	0	0	0	0	0	21	0	21	21
Jun-96	3	28	0	31	0	0	0	0	0	30	0	30	61
Jul-96	6	10	0	16	8	19	0	27	21	19	0	40	83
Aug-96	19	21	0	40	0	0	0	0	0	0	0	0	40
Sep-96	11	21	0	32	0	0	0	0	11	20	0	31	63
Oct-96	29	16	0	45	0	0	0	0	0	0	0	0	45
Nov-96	9	20	0	29	0	0	0	0	0	0	0	0	29
Dec-96	10	18	0	28	0	0	0	0	0	0	0	0	28
Jan-97	43	39	0	82	78	80	2	160	9	12	0	21	263
Feb-97	43	77	0	120	0	0	0	0	18	28	1	47	167
Mar-97	51	95	1	147	17	52	0	69	3	6	0	9	225
Apr-97	40	70	0	110	24	54	0	78	28	55	6	89	277
May-97	49	71	50	170	44	47	0	91	65	57	0	122	383
Jun-97	70	106	0	176	0	0	0	0	56	67	0	123	299
Jul-97	56	85	0	141	0	0	0	0	94	87	0	181	322
Aug-97	74	90	0	164	0	0	0	0	19	61	0	80	244
Sep-97	21	31	0	52	0	0	0	0	73	120	0	193	245
Oct-97	45	57	0	102	0	0	0	0	51	95	0	146	248
Nov-97	21	45	0	66	0	0	0	0	53	72	0	125	191
Dec-97	12	24	0	36	10	20	0	30	0	0	0	0	66
Total	612	924	51	1587	181	272	2	455	501	750	7	1258	3300

size (± s.d.) of oocytes at these developmental stages is given in Table 4. As unyolked oocytes developed to Stage III (~200 μm) they became larger than the standing stock of oocytes (~100 μm). After they had reached the yolked stage (Stage IV), they were easily distinguishable from the unyolked oocytes by their larger size (400–700 μm). These were the oocytes that were to be spawned during the oncoming season and provided the evidence of determinate annual fecundity. As they developed further (Stage V onwards), a bimodal distribution in the diameter of the yolked oocyte became apparent. The larger oocytes (>800 μm) were those in the 'batch' that had begun to hydrate before spawning. The smaller yolked oocytes (400–800 μm) were those to be spawned in subsequent batches. When hydration was complete and spawning was imminent (Stage VI), these oocytes ranged from 1290 μm to 1520 μm. After these were spawned, a subsequent batch of the yolked oocytes would hydrate in preparation for spawning.

Fecundity

Annual fecundity (AF) increased exponentially with length (L), ranging from 0.43 to 1.35 million oocytes per fish (Fig. 9). Although annual fecundity varied considerably for a given length, linear regression of the log-transformed data was statistically significant ($F_{1,35} = 36.22$, $P < 0.0001$, $R^2 = 0.51$) yielding the equation: $\ln[AF] = 2.896 \times \ln L + 2.458$. Similarly, batch fecundity (BF) ranged from 0.21 to 0.36 million oocytes per fish and the regression for the log-

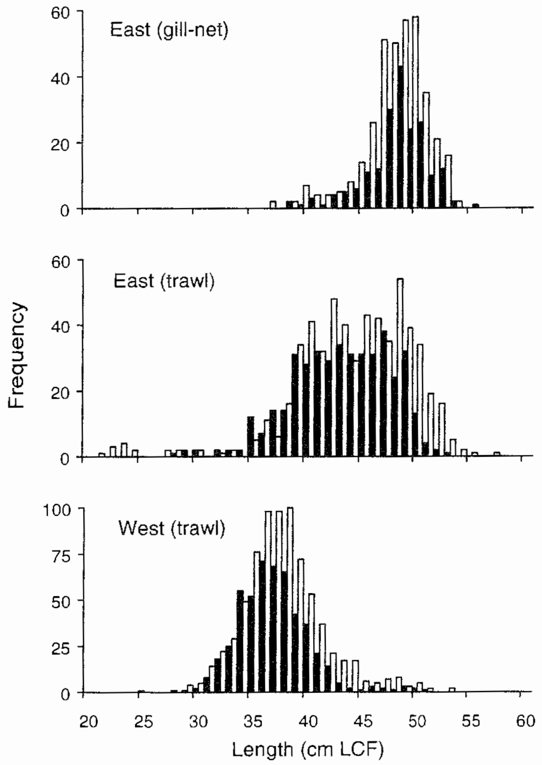


Fig. 4. Length–frequency distributions of (■) male and (□) female blue warehou collected between January and December 1997 from commercial gill-net and trawl catches in the East and trawl catches in the West.

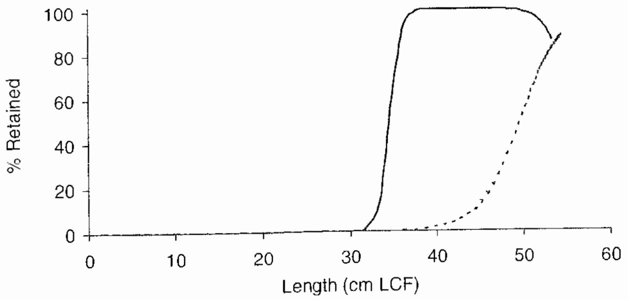


Fig. 5. Selectivity ogives used in the per-recruit analyses for (—) trawl and (---) gill-net fishing methods. The ogives incorporate the selectivity of the gear as well as the availability of fish to capture by that gear.

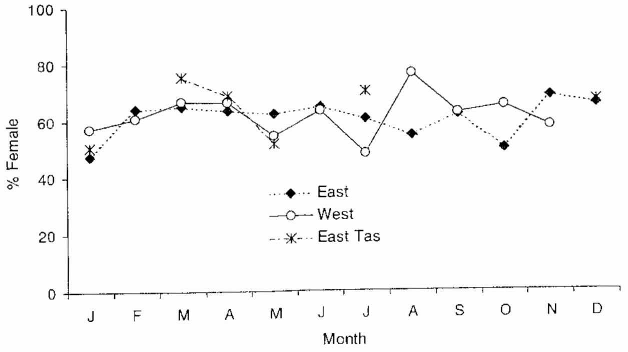


Fig. 6. Percentage of female blue warehou in monthly samples collected from the East, West and East Tasmanian regions between January and December 1997.

transformed data was ln[BF] = 2.614 × ln$L$ + 2.366 ($F_{1,8}$ = 7.56, P <0.05, R^2 = 0.49). Comparison of these two regressions revealed that around three batches of eggs were spawned each year.

The average relative fecundity was 417 oocytes (± 99 s.d.) g^{-1} (gutted weight) and ranged between 200 and 780 oocytes g^{-1}. Relative fecundity was not significantly related to fish length ($F_{1,34}$ = 0.08648, P >0.77, R^2 = 0.002).

Size at maturity

No females <30 cm length were mature. The logistic equation for the maturity ogive of female blue warehou was

$$\% \text{ mature} = 100 / (1 + e^{0.436\,(35.82 - L)}).$$

This indicates that L_{m50} was ~36 cm and 90% were mature at 40 cm (Fig. 10). Using the inverse von Bertalanffy equation, the age at which 50% of the population would be mature (t_{m50}) was estimated at 3.67 years. Females in spawning condition usually had a GSI of >5%, most females greater than 45 cm had a GSI of >10% and some had a GSI of ~20%. GSI values in spawning fish were variable because some individuals had already shed an unknown number of oocytes, resulting in loss of ovary mass (partially spent). Generally, GSI values for spawning females were considerably higher than those for spawning males, which rarely exceeded 10%.

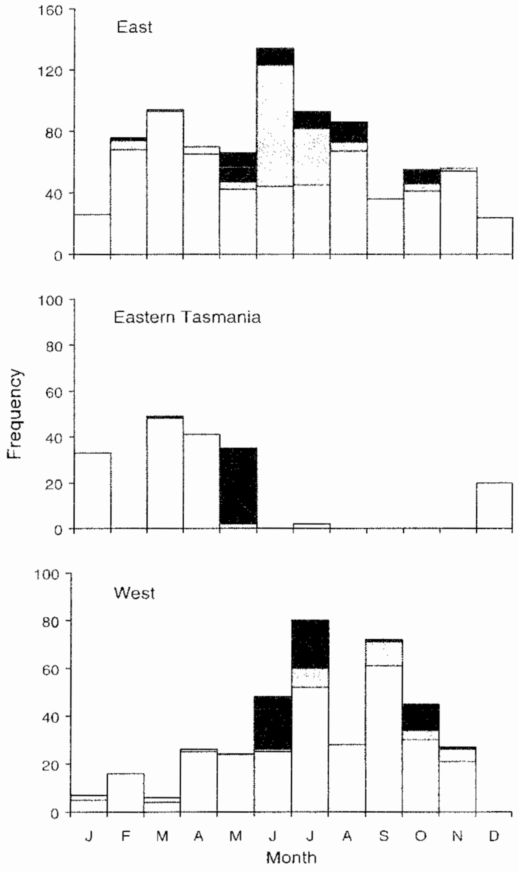


Fig. 7. Frequency of mature female blue warehou with gonads in spawning condition (shaded columns, Stage V and VI), spent (black, Stage VII) and other non-spawning stages (white, Stage I, IIa, IIb, III and IV), in each of the three regions.

Per-recruit analyses

The ageing estimates and von Bertalanffy growth parameters used in this study were based on unpublished data. A range of natural mortality estimates resulted from application of the various life-history methods. These were 0.30 year^{-1} (based on Hoenig 1983), 0.41 year^{-1} (Pauly 1980), 0.44 year^{-1} (Rikhter and Efanov 1976) and 0.45 year^{-1} (Beverton and Holt 1957). Although the results of the per-recruit analyses were influenced by this range of natural mortality estimates, in a situation with no fishing mortality the peak in eggs-per-recruit occurred for fish at ~40 cm (Fig. 11*upper*) or between 4 and 5 years old (Fig. 11*lower*) for all estimates of natural mortality.

For further per-recruit analyses, a natural mortality estimate of 0.45 year^{-1} was chosen (the same as the base case used by Smith 1999) and the effect of fishing by trawl

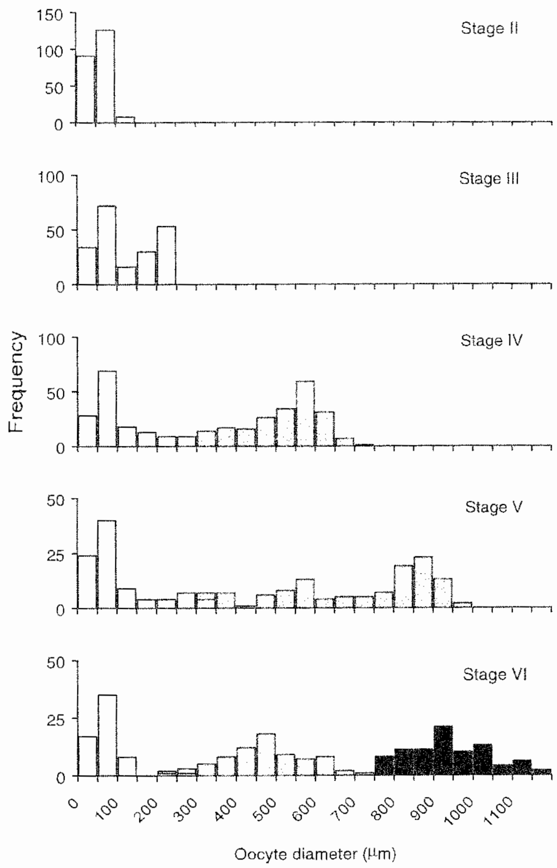


Fig. 8. Frequency distribution of unyolked (white columns), yolked (shaded columns) and hydrated (black columns) oocyte diameter (μm) for Stage II to Stage VI ovaries. Data pooled across regions.

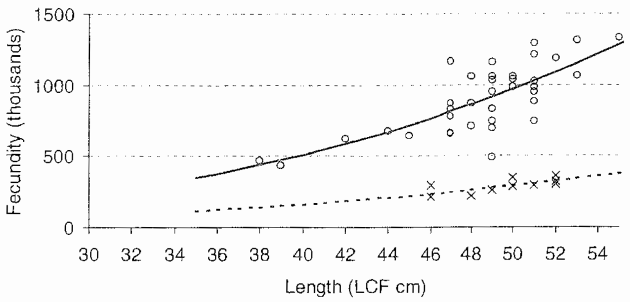


Fig. 9. Relationship of (○) annual fecundity and (×) batch fecundity to length (LCF, cm) of female blue warehou.

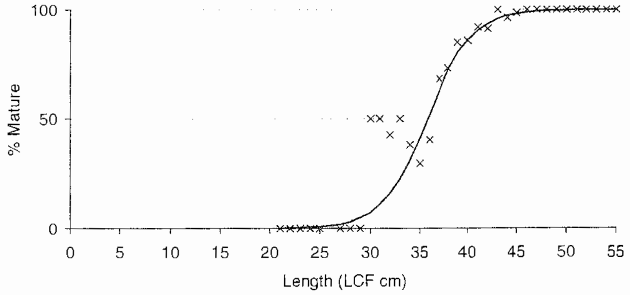


Fig. 10. Maturity ogive for female blue warehou plotted against length (LCF, cm). Data points (×) represent the percent mature in 1 cm length-classes. Analyses were performed on data pooled over year and area.

and gill-net methods was compared. Estimates of yield-per-recruit and eggs-per-recruit for a range of fishing mortalities ($F = 0$ to $F = 2$ year^{-1}) are shown for populations fished by trawls and gill-nets (Fig. 12). A plot of yield-per-recruit against eggs-per-recruit (Fig. 13) aided in the comparison of the effects of the two fishing methods, and revealed that although they are similar, fishing by gill-net had less effect on eggs-per-recruit remaining in the population for a given yield-per-recruit. Furthermore, although higher yield-per-recruit could be obtained by trawl fishing, this method also had the potential to reduce eggs-per-recruit significantly more than gill-nets.

Table 4. GSI, diameter of oocytes dissociated from whole gonads (whole) and diameter of oocytes prepared in histological sections (histo.) for the different stages of female reproductive development
Values are mean ± s.d.

Stage	Gonadosomatic index	*n*	Oocyte diameter (whole)	*n*	Oocyte diameter (histo.)	*n*
I	0.13 ± 0.12	75				
II	0.84 ± 0.56	976			66 ± 28	592
III	2.21 ± 1.40	341	196 ± 60	500	241 ± 40	138
IV	4.97 ± 1.43	291	585 ± 171	2500	510 ± 100	317
V	7.78 ± 2.69	80	810 ± 294	1000	821 ± 107	77
VI	12.36 ± 3.68	109	994 ± 323	1000	891 ± 136	105
VII	1.19 ± 1.14	155				

Discussion

Considerable spatial and temporal structuring is evident within the blue warehou fishery off south-eastern Australia (Smith *et al.* 1998). Although there have been no studies on the stock structure of blue warehou in Australian waters, the species is assumed to comprise a single stock for fisheries assessment and management purposes. This is because blue warehou, like spotted warehou (*S. punctata*), are known to undertake major migrations (Gavrilov and Markina 1979) and they are generally perceived to be highly mobile species with a broad distribution of breeding localities. Blue warehou have been tagged in south-eastern Australian waters (Knuckey *et al.* 1999), but lack of tag recaptures precluded conclusive information on movement patterns. Nevertheless, the present study revealed that blue warehou spawn over a wide range of areas within the SEF. These results are supported by a recent study of its larval distribution (Bruce *et al.* 2001) in which concentrations of

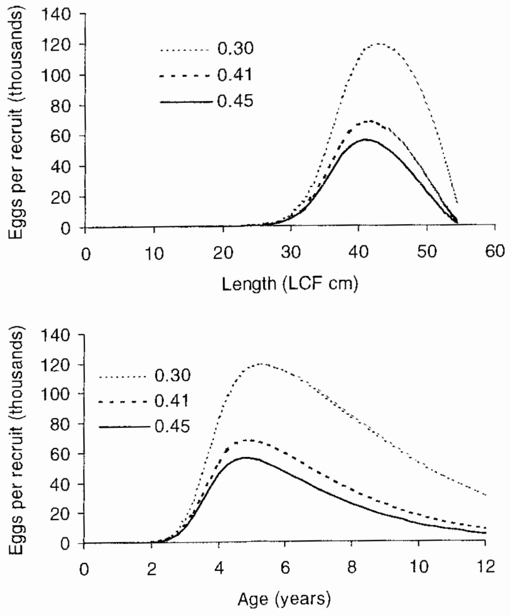


Fig. 11. Eggs-per-recruit estimates for female blue warehou plotted against *(upper)* length and *(lower)* age for a range of natural mortality estimates. No fishing mortality has been incorporated into these analyses.

young larvae were found from Kangaroo Island in South Australia to southern Tasmania, with a major concentration off the north-western coast of Tasmania and another off the eastern Victoria/New South Wales border. Interestingly, the region off north-western Tasmania, characterized by the highest concentrations of larvae, does not form a major part of the commercial fishery for blue warehou and was not sampled in the present study. Furthermore, only low larval densities were found off the east coast of Tasmania and in eastern Bass Strait (Bruce *et al.* 2001) and there is no major fishing in these areas during the spawning season. Although the present study found spent fish off eastern Tasmania in May, the lack of samples from winter and spring limited firm conclusions about spawning in this area.

In the present study, there was no spatial or temporal difference in the spawning characteristics of males and females. There were, however, persistently more females caught than males. This can not be explained on the basis of the present results, and would not result from biased selectivity towards larger females. The preponderance of females remained throughout the year and across the different areas and methods in the fishery. Assuming the sex ratio of the entire population is not skewed towards females, further research would be needed to determine whether any characteristic of the distribution, behaviour or some other aspect of the life history makes males less vulnerable to capture in the SEF.

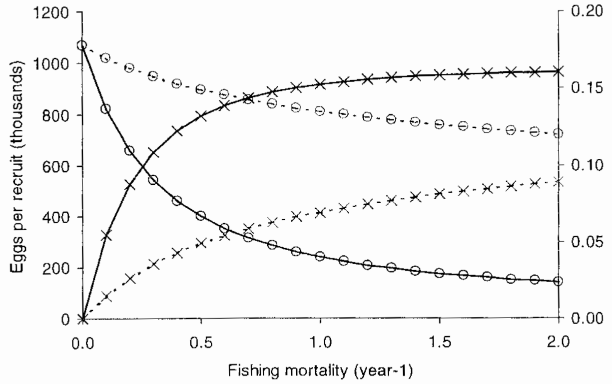


Fig. 12. Eggs-per-recruit (○) and yield per recruit (x) of female blue warehou plotted against a range of fishing mortalities ($F = 0$ to $F = 2$ year^{-1}) for trawl (——) and gill-net (---) fishing methods.

Fig. 13. Yield-per-recruit of female blue warehou plotted against eggs-per-recruit over a range of fishing mortalities ($F = 0$ to $F = 2$ year^{-1}) for trawl (——) and gill-net (---) fishing methods.

A previous study on the GSI of blue warehou established that they spawned during winter in western Bass Strait (Smith *et al.* 1995). Smith (1994) noted that this was slightly earlier than the spring–summer spawning period observed in New Zealand (Gavrilov 1976). The macroscopic and histological analysis of gonads in the present study confirmed that the main spawning period in Australian waters extends from winter to spring.

Other studies have revealed that the ovaries of spawning females display histological evidence of past spawning (postovulatory follicles) or imminent spawning (hydrated oocytes or migratory-nucleus-stage oocytes (West 1990; Karlou-Riga and Economidis 1997). Postovulatory follicles are rapidly reabsorbed in several temperate species (Marshall *et al.* 1993) and are often difficult to identify one to two days after spawning (e.g. Hunter and Goldberg 1980; Melo 1994; Schaefer 1996), after which time they may not be distinguished from intermediate stages of atretic oocytes (Hunter and Macewicz 1985*a*). The occurrence of atretic ova marks the end of spawning (Hunter and Macewicz 1985*b*) and is associated with spent ovaries. Hunter and Macewicz (1980) suggested that the best indicator of the time of spawning was the occurrence of both hydrated eggs and postovulatory follicles.

On the basis of these criteria, the present study established that the main spawning period in the East occurred during May–August, and this was about a month earlier than in the West (June–October). Very few spawning fish were found outside these months. These results are consistent with those of Bruce *et al.* (2001) who used back-calculation of larval ages and deduced a winter or winter–spring spawning period and also noted that spawning occurred earlier in the East than in the West. Although the main fishing season in the West approximately corresponds to the spawning season, most of the catches in the East are taken after the main spawning period. The large spatial separation between the main spawning areas in the East and West and their different spawning times lead Bruce *et al.* (2001) to conclude that these could be considered as separate spawning stocks.

Around 90% of blue warehou were mature at 40 cm and the L_{m50} was ~36 cm LCF, which corresponds to fish of 3–4 years old. All fish <30 cm were immature. Because of the difficulty in distinguishing between the gonads of males that were maturing for the first time and the redeveloping gonads of mature fish, a maturity ogive could not be established for males. Nevertheless, the GSI data indicated that males develop to maturity at a size similar to that of females. The size frequency of fish caught during this study and those from more extensive sampling programmes (Knuckey and Sporcic 1999) show that few fish <30 cm are caught by commercial vessels in the SEF and the majority are >35 cm. As a consequence, most of the commercial blue warehou catch would consist of mature fish.

The size at maturity determined in the present study is somewhat lower than that found in previous studies. A size at maturity of 40–45 cm LCF has been recorded for blue warehou in New Zealand waters (Gavrilov and Markina 1979). On the basis of a survey in western Bass Strait during the late 1980s, Smith *et al.* (1995) also reported that females mature between 40 and 45 cm. This conclusion was based largely on GSI information from a small number of fish (~250) caught between June and September. Without detailed macroscopic examination and/or histological information, however, it is difficult to distinguish fish with redeveloping gonads from those maturing for the first time. In both cases these fish will have low GSIs, and size at maturity values based on analysis of GSI data alone could be overestimated if fish with redeveloping gonads were mistakenly classified as immature.

The high relative fecundity of blue warehou (417 ± 99 oocytes g^{-1}) is similar to blue-eye trevalla (*Hyperoglyphe antarctica*, 480 ± 125 oocytes g^{-1}), another centrolophid found in these waters (Baelde 1996). Similarly, both of these fish are group-synchronous batch spawners with a determinate annual fecundity. The annual fecundity of blue warehou increases exponentially with the length of females (0.43–1.35 million oocytes per fish between 38 and 55 cm LCF). These oocytes are released in about three large batches of 0.21–0.36 million oocytes per fish, increasing with length of females. Because postovulatory follicles usually persist in fish ovaries for only a short period (Hunter and Goldberg 1980; Macewicz and Hunter 1993; Melo 1994), the co-occurrence of postovulatory follicles and ripe oocytes in blue warehou ovaries suggests that successive batches of oocytes may be released within a few days. More intensive sampling over short time periods within the spawning season would be required to prove this.

Implications for the fishery

Recruitment, via reproduction, is the means by which the resource is renewed. If indiscriminate harvesting of a population occurs, the number of animals that reach maturity can be reduced to an extent at which the reproductive capacity of the population is diminished. One way of reducing this possibility is to ensure that minimal fishing pressure is applied to the population before the fish reach maturity. Often, this is achieved by setting restrictions on mesh sizes used to catch the fish. Within the SEF, blue warehou have been caught predominantly by trawl and gill-nets with minimum mesh sizes of 90 mm for the codend of trawls and 150 mm for monofilament gill-nets. A total allowable catch (TAC) managed through a system of individual transferable quotas was introduced into the trawl sector in 1993. During 1998 a global TAC was introduced (across the trawl and non-trawl sectors) and leasing of quota between sectors was enabled. This, combined with the different selectivity of the two types of gears, has important implications for the fishery in terms of the potential effect on the reproductive capacity of the stock.

Although most blue warehou caught in the commercial fishery are mature (present study), those caught in the East by the gill-net sector are generally larger and older than those caught by the trawl sector throughout the fishery (Smith 1999). This primarily reflects the difference in selectivity between the trawl codend mesh and the gill-nets, but may also be influenced by the tendency for fish caught in the East to be larger than those caught in the West (present study; Knuckey and Sporcic 1999). In Australian waters, blue warehou live to a maximum age of ~10 years (Smith and Wayte 2000). On the basis of the present study, at the size/age that the fish are caught by gill-nets they have less reproductive potential than the newly matured younger fish captured in the trawl fishery. In recent years, catches from the gill-net fishery have been poor (Smith and Wayte 2000), and under the global TAC most leasing of quota has been from the non-trawl sector to the trawl sector (Australian Fisheries Management Authority, unpublished). On a purely per-recruit basis, if this non-trawl quota were caught by trawl operators, it would potentially reduce the reproductive capacity of the blue warehou stock to a greater degree than if the quota were caught by gill-nets. Although fishery managers should consider this point, it is a simplistic one. Per-recruit analyses do not incorporate information about the actual levels of recruitment in a fishery (Sainsbury 1992), which is one of the main sources of variability in the total yield from a fishery (MacLennan 1993). Hence, although gill-net fishing has less potential to affect the reproductive potential of the population and provides more yield-per-recruit for a given reduction in eggs-per-recruit, there have been significant declines in the abundance of the larger fish targeted by these gill-nets and a general acceptance that the high gill-net catches during the early 1990s were not sustainable. Moreover, the blue warehou population is subject to fishing by the combined effort from the two fishing methods, and it is not appropriate to consider the effects of each fishing method in isolation. More recently, there has also been a general decline in blue warehou catches by the trawl sector, and more sophisticated models of the fishery are required. Models that integrate the information on maturity, fecundity and seasonal reproductive patterns gained from the present study with other factors such as variable recruitment, the spatial structuring of the fishery and inter-sectorial leasing of quota are being developed and applied (Punt 1999). The results of these models are helping to support management decisions that ensure the long-term viability of blue warehou stocks as an important component of the SEF.

Acknowledgments

The authors are grateful to Ken Smith, David McKeown, Pam Oliveiro, Graeme Cottier and Sharon Berrie for collection of samples for this project. Sandy Morison and other members of Central Ageing Facility provided the ageing data. Miriana Sporcic and André Punt advised on data analysis. Editorial comments were provided by David Smith. We also thank Annie Hughes of Deakin University for the histological preparations and Peter Hooper of CSIRO Animal Health Laboratory for the photographs of histological slides. This research study was jointly funded by the Marine and Freshwater Resources Institute and the Fisheries Research Development Corporation (Project No. 96/142).

References

Baelde, P. (1996). Biology and dynamics of the reproduction of the blue-eye trevalla, *Hyperoglyphe antarctica* (Centrolophidae), off Tasmania, southern Australia. *Fishery Bulletin (US)* **94**, 199–211.

Bell, J. D., Lyle, J. M., Bulman, C. M., Graham, K. J., Newton G. M., and Smith, D. C. (1992). Spatial variation in reproduction, and occurrence of non-reproductive adults, in orange roughy, *Hoplostethus atlanticus* Collet (Trachichthyidae), from south-eastern Australia. *Journal of Fish Biology* **40**, 107–22.

Bertalanffy, L. von (1938). A quantitative theory of organic growth. *Human Biology* **10**, 181–213.

Beverton, R. J. H., and Holt, S. J. (1957). On the dynamics of exploited fish populations. Fisheries Investment Series 2, Vol. 19. (UK Ministry of Agriculture and Fisheries: London.)

Bruce, B. D., Neira, F. J., and Bradford, R. W. (2001). Larval distribution and abundance of blue and spotted warehous (*Seriolella brama* and *S. punctata*: Centrolophidae) in south-eastern Australia. *Marine and Freshwater Research* **52**, 631–6.

Davis, T. L. O. (1977). Reproductive biology of the freshwater catfish, *Tandanus tandanus* Mitchell, in the Gwydir River, Australia. I. Structure of the gonads. *Australian Journal of Marine and Freshwater Research* **28**, 139–58.

DeMartini, E. E., and Fountain, R. K. (1981). Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus:* attributes representative of serial spawning fishes. *Fishery Bulletin (US)* **79**, 547–60.

Forberg, K. G. (1982). A histological study of development of oocytes in capelin, *Mullotus villosus villosus* (Muller). *Journal of Fish Biology* **20**, 143–54.

Gavrilov, G. M. (1976). The sexual cycle, spawning characteristics and fertility of the silver fish, *Seriolella maculata* Forster. News of the Pacific Ocean Scientific Research Institute of Fishing and Oceanography (TINRO) 100, 58–68.

Gavrilov, G. M., and Markina, N. P. (1979). The feeding ecology of fishes of the genus *Seriolella* (fam: Nomidae) on the New Zealand Plateau. *Journal of Ichthyology* **19**, 128–35.

Gooley, G. J., Anderson, T. A., and Appleford, P. (1995). Aspects of the reproductive cycle and gonadal development of Murray cod, *Maccullochella peelii peelii* (Mitchell) (Percichthyidae), in Lake Charlegrark and adjacent farm ponds, Victoria, Australia. *Marine and Freshwater Research* **46**, 723–8.

Hoenig, J. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin (US)* **82**, 898–903.

Hunter, J. R., and Goldberg, S. R. (1980). Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax. Fishery Bulletin (US)* **77**, 641–52.

Hunter, J. R., and Macewicz, B. J. (1980). Sexual maturity, batch fecundity, spawning frequency and temporal pattern in the northern anchovy *Engraulis mordax*, during the 1979 spawning season. California Cooperative Oceanic Fisheries Investigations Reports No. 21, 139–49.

Hunter, J. R., and Macewicz, B. J. (1985*a*). Measurement of spawning frequency in multiple spawning fishes. In 'An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*'. (Ed. R. Lasker.) US Department of Commerce, NOAA Technical Report NMFS 36, 79–94.

Hunter, J. R., and Macewicz, B. J. (1985*b*). Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax. Fishery Bulletin (US)* **83**, 119–36.

Hunter, J. R., Lo, N. C. H., and Leong, R. J. H. (1985). Batch fecundity in multiple spawning fishes. In 'An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*'. (Ed. R. Lasker.) US Department of Commerce, NOAA Technical Report NMFS 36, 67–77.

Jensen, A. L. (1982). Adjusting fishery catch curves for trawl selection using the logistic distribution. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **40**(1), 17–20.

Karlou-Riga, C., and Economidis, P. S. (1997). Spawning frequency and batch fecundity of horse mackerel, *Trachurus trachurus* (L.), in the Saronikos Gulf (Greece). *Journal of Applied Ichthyology* **13**, 97–104.

Knuckey, I. A., and Sporcic, M. I. (1999). South East Fishery Integrated Scientific Monitoring Program – 1998 Report to the South East Fishery Assessment Group. 80 pp. (Australian Fisheries Management Authority: Canberra.)

Knuckey, I. A., MacDonald, C. M., Lyle, J. M., and Smith, D. C. (1999). Movement and exploitation rates of blue and spotted warehou – a pilot tagging study. Final Report to the Fisheries Research and Development Corporation [Canberra]. 49 pp.

Luna, L. G. (1968). 'Manual of Histological Staining Methods of the Armed Forces Institute of Pathology.' 3rd Edn. (McGraw-Hill: Sydney.)

MacDonald, C. M., and Smith D. C. (1996). Blue warehou 1995, Stock Assessment Report, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Macewicz, B. J., and Hunter, J. R. (1993). Spawning frequency and batch fecundity of jack mackerel, *Trachurus symmetricus*, off California during 1991. CalCOFI Report No. 34, 112–21.

MacLennan, D. N. (1993) Gear selectivity and the variation of yield. Council Meeting of the International Council for the Exploration of the Sea [Dublin (Eire)] [23 Sep. – 1 Oct. 1993] Copenhagen, Denmark ICES 1993, ICES-CM–1993/D:32. 11 pp.

Marshall, J., Pullen, G., and Jordan, A. (1993). Reproductive biology and sexual maturity of female jack mackerel, *Trachurus declivis* (Jenyns), in eastern Tasmania waters. *Australian Journal of Marine and Freshwater Research* **44**, 799–809.

Melo, Y. C. (1994). Multiple spawning of the anchovy *Engraulis capensis*. *South African Journal Marine Science* **14**, 313–19.

Morison, A. K., Robertson, S. G., and Smith, D. C. (1998). An integrated system for production fish ageing: image analysis and quality assurance. *North American Journal of Fisheries Management* **18**, 587–98.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer., **39**(3), 175–92.

Pauly, D. (1984). Length-converted catch curves. A powerful tool for fisheries research in the tropics. (Part II). *ICLARM Fishbyte* **2**(1), 17–19.

Punt, A. (1999). An assessment of blue warehou for 1999 based on integrated analysis. Document submitted to the 1999 Blue Warehou Assessment Group. 34 pp. (Australian Fisheries Management Authority: Canberra.)

Ricker, W. E. (1945). A method of estimating minimum size limits for obtaining maximum yield. Copeia **2**, 84–94.

Rikhter, V. A., and Efanov, V. N. (1976). On one of the approaches to estimation of natural mortality of fish populations. International Commission for the Northwest Atlantic Fisheries Research Document No. 76. VI/8. 12 pp.

Sainsbury, K. (1992). Yield-per-recruit based assessment methods. Yield, value, biomass and eggs per recruit – the $F_{0.1}$ management strategy. In 'The Measurement of Age and Growth in Fish and Shellfish'. Australian Society for Fish Biology Workshop, 22–23 August 1990. (Ed. D. A. Hancock.) Bureau of Rural Resources Proceedings No. 12. 199–204.

Sanders, M. J. (1995). Introduction to Thompson and Bell yield analysis using Excel spreadsheets. FAO Fisheries Circular No. 895. (FAO: Rome.) 21 pp.

Schaefer, K. M. (1996). Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean. *Fishery Bulletin (US)* **94**, 98–112.

Smith, A. D. M., and Wayte, S. E. (Eds) (2000). The South East Fishery 1999, Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Smith, D., Huber, D., Woolcock, J., Withell, A., and Williams, S. (1995). Western Bass Strait trawl fishery assessment program. Final report to the Fisheries Research and Development Corporation [Canberra]. Project 86/39, 130 pp.

Smith, D. C. (1994). Blue warehou. In 'The South East Trawl Fishery – A Scientific Review with Particular Reference to Quota Management'. (Ed. R. D. J. Tilzey.) (Bureau of Resource Sciences: Canberra.)

Smith, D. C. (1995). Blue warehou 1994 Stock Assessment Report, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Smith, D. C. (1999). Blue warehou 1999 Stock Assessment Report, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Smith, D. C., O'Brien C., and Roob, R. (1998). Detailed analysis of blue warehou catch and effort data. Final report to the Australian Fisheries Management Authority. ARF Project 95/96–18, 34 pp.

Staples, D., and Tilzey, R. (1994). South east fishery – quota species. In 'Fishery Status Report 1993, Resources Assessments of Australian Commonwealth Fisheries'. (Eds K. McLouglin, D. Staples and M. Maliel.) pp. 61–8. (Bureau of Resource Sciences: Canberra.)

Thompson W. F., and Bell, F. H. (1934). Biological statistics of the Pacific halibut fishery. 2. Effect of changes in intensity upon total yield and yield per unit of gear. Report of the International Fisheries (Pacific halibut) Commission No. 8. 49 pp.

Watson, J. J., Priede, I. G., Witthames, P. R., and Owori-Wadunde, A. (1992). Batch fecundity of Atlantic mackerel, *Scomber scomberus* L. *Journal of Fish Biology* **40**, 591–8.

West, G. (1990). Methods of assessing ovarian development in fishes: a review. *Australian Journal of Marine and Freshwater Research* **41**, 199–222.

Yamamoto, K. (1956). Studies on the formation of fish eggs. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. *Faculty of Science Hokkaido University Series* **6**(12), 362–73.

Manuscript received 16 February 2000; revised 10 November 2000 and 14 February 2001; accepted 14 February 2001

Mar. Freshwater Res., 2001, **52**, 589–601

Reproductive biology, early life-history and settlement distribution of sand flathead (*Platycephalus bassensis*) in Tasmania

Alan R. Jordan

Marine Research Laboratories, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Crayfish Point, Taroona, Tas. 7053, Australia

Abstract. The life-history ecology of *P. bassensis* was examined to determine the spatial and temporal patterns of spawning, larval transport and settlement distribution in coastal and continental shelf waters of southern and eastern Tasmania. Larval development is characterized by a large size at flexion and pelvic and dorsal fin formation, lightly pigmented trunk and tail and the absence of strong teeth on the roof of the mouth or lower jaw. The distribution of spawning fish and larvae and patterns of hydrography indicate that spawning occurs throughout estuaries, coastal embayments and inshore shelf waters of southern and eastern Tasmania. Larvae are concentrated in mid waters, which retain larvae inshore because cross-shelf subsurface currents are predominantly onshore. Spawning in *P. bassensis* occurred for up to six months between October and March. The broad range of lengths of 0+ fish in every month indicates that settlement occurred over an extended period, reflecting the protracted spawning period. Juveniles showed a preference for unvegetated habitats in nearshore waters, compared with beds of the seagrass *Heterozostera tasmanica.* Size compositions of 0+ fish indicate the presence of several cohorts in most months; this is discussed in terms of early life-history strategy and availability of settlement habitats.

Introduction

The Family Platycephalidae (flatheads) contains around 60 species found primarily in coastal and estuarine waters of the Indo-Pacific region. In temperate Australian waters the family is represented by 13 species many of which are of considerable commercial and recreational importance (Kailola *et al.* 1993). Despite the diversity and widespread distribution of the platycephalids, the reproductive biology and early life history stages have been poorly described. Larval descriptions have been given for *Platycephalus indicus* and *Onigocia spinosa* from Japan (Kojima 1988) and *P. speculator* (Hyndes *et al.* 1992) and *P. fuscus* (Neira and Miskiewicz 1998) from southern Australia, with larvae characterized by a large depressed head with extensive spination, large, fan-shaped pectoral fins and 25–28 myomeres.

Two unidentified species of platycephalid larvae were identified in Port Phillip Bay, Vic., with larvae present in most months of the year (Jenkins 1986). The distribution of *Platycephalus* spp. and *P. fuscus* larvae has been reported from coastal waters off New South Wales (Gray *et al.* 1992), with evidence that their vertical distribution was independent of the thermocline (Gray 1996). There are limited data on the reproductive biology of *Neoplatycephalus richardsoni* (Fairbridge 1951; Jordan 1997), *P. speculator* (Hyndes *et al.* 1992) and *P. bassensis*, *P. fuscus* and *P. speculator* (Brown 1978). In the most detailed study, Hyndes *et al.* (1992) found *P. speculator* to be a multiple spawner with spawning occurring in estuaries during summer and early autumn (December–March).

Platycephalus bassensis is a common demersal species from the central coast of New South Wales to eastern South Australia, but is most abundant in southern New South Wales, Victoria and Tasmania (Gomon *et al.* 1994). It occurs on sandy and muddy substrata down to 100 m but is found mainly in shallow coastal waters of <65 m. Commercial and recreational fishing for *P. bassensis* occurs throughout Tasmanian and Victorian waters (Neira *et al.* 1997; Lyle and Jordan 1998). Spawning in *P. bassensis* is reported to occur between August and October in Port Phillip Bay, Vic. (Brown 1978), but despite their presence on the continental shelf, spawning has not been documented in this region.

Most species of platycephalids common in temperate estuarine and coastal waters of Australia show a preference for unvegetated habitats, although the lack of studies describing patterns of abundance and distribution often reflects the low abundance of individual species (Edgar and Shaw 1995; Gray *et al.* 1996; Jenkins and Wheatley 1997). Although juvenile *P. bassensis* have been shown to occur in shallow unvegetated habitats (<3 m deep) in Tasmania (Last 1983), their distribution in deeper subtidal unvegetated and seagrass habitats has not been examined.

10.1071/MF99155 1323-1650/01/040589

Such deeper habitats form a substantial part of the coastal region of Tasmania, with beds of the seagrass *Heterozostera tasmanica* common in depths down to 7 m and unvegetated habitats dominant in marine embayments and estuaries.

The aim of this paper is to (1) describe the larval development stages of *P. bassensis*, (2) determine the temporal and spatial patterns of spawning through examining patterns in gonadal development and larval distributions, and (3) examine habitat preference and temporal patterns in abundance in inshore embayments and estuaries (0–15 m) of southern and eastern Tasmania.

Methods

Adult and juvenile surveys

Platycephalus bassensis was caught from *Heterozostera tasmanica* and unvegetated habitats in inshore waters (<15 m deep) in three areas along the east coast of Tasmania: Norfolk Bay, Prosser Bay and Georges Bay (Table 1, Fig. 1). In Norfolk Bay, *P. bassensis* was caught at three *H. tasmanica* and three unvegetated sites every 2 months from February 1995 to December 1996. Four sites were sampled in Georges Bay and two in Prosser Bay every 3 months from February to October 1995. Juvenile *P. bassensis* were sampled at each site with a beam trawl with an opening of 2.0 × 0.9 m and a 5 m long net with a 7 mm codend liner mesh. Large and more mobile *P. bassensis* were sampled at selected sites with 30 m long multi-panel gillnets comprising three randomly placed 10 m panels of increasing gillmesh size (64, 89 and 108 mm). Two multi-panel gillnets were set overnight at two sites in each area on each sampling occasion. At each station, *P. bassensis* were sorted and retained for biological processing in the laboratory.

Finer temporal patterns of recruitment of juvenile *P. bassensis* were also examined from beam trawl sampling conducted every two months from March to July 1996 and then monthly until May 1997 in North West Bay (NW Bay), south-eastern Tasmania (Fig. 2). The sampling site was unvegetated and consisted of soft-mud in depths of 3–10 m.

Plankton surveys

The distribution of platycephalid larvae on the shelf of eastern Tasmania was determined from plankton samples collected at three fixed stations on five transects from Bicheno in the north (T1) to Marion Bay in the south (T5) (Fig. 2). Platycephalid larvae were sorted from samples taken on two surveys in January 1989 and two in January 1990. Transects consisted of three stations designated as inner-shelf (at a bottom depth of 30–50 m), mid-shelf (depth 70–100 m), and shelf break (0.5 naut.miles inshore of the shelf break at an average depth of 150 m).

Ichthyoplankton were collected with a 45 cm diameter bongo net with 500 μm mesh. Each station consisted of an oblique tow to a maximum depth of 100 m (bottom depth permitting), at a tow speed of ~3 knots. At each station the net was sent to the required depth quickly, held there for 1–2 min and then retrieved on an oblique path. Filtered volume was estimated with calibrated flowmeters. Samples from one side of the bongo were preserved in 95% ethanol, and the

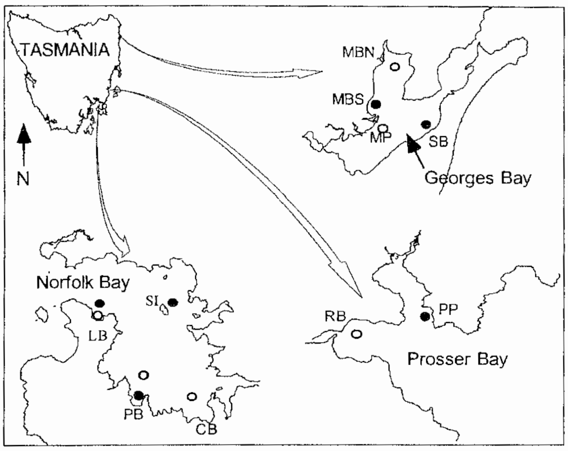


Fig. 1. Position of beam trawl and gill-net sampling sites in Norfolk Bay, Prosser Bay and Georges Bay, eastern Tasmania. ●, *Heterozostera tasmanica*; ○, unvegetated sites.

Table 1. Habitat characteristics and gear deployed at sites sampled in Norfolk Bay, Georges Bay and Prosser Bay

Site codes refer to those in Fig. 1. Beam trawl (BT) and gillnet (GN)

Area/Site	Habitat	Depth (m)	Gear deployed
Norfolk Bay			
Cascade Bay (CB)	Mud	8–12	BT, GN
Prices Bay (PB)	*Heterozostera*	3–6	BT
Prices Bay (PB)	Mud	8–12	BT
Lime Bay (LB)	*Heterozostera*	3–6	BT, GN
Lime Bay (LB)	Sand	1–3	BT
Smooth Island (SI)	*Heterozostera*	4–6	BT
Georges Bay			
Steiglitz Beach (SB)	*Heterozostera*	2–5	BT, GN
McDonalds Pt. (MP)	Mud	8–12	BT
Moulting Bay N (MBN)	Mud	3–5	BT, GN
Moulting Bay S (MBS)	*Heterozostera*	2–4	BT
Prosser Bay			
Paddys Point (PP)	*Heterozostera*	3–5	BT, GN
Raspins Beach (RB)	Sand	2–4	BT, GN

other in buffered 4% seawater formaldehyde. Sampling was restricted to daylight hours (~0600–2000 hours). Temperature (±0.1°C) and depth (±0.1 m) were recorded at each station with a temperature/depth probe attached to the net during each tow. Surface temperatures were recorded from an on-board temperature recorder (±0.1°C). The vertical distribution of larvae was assessed in late January 1989 on the mid-shelf station on Transect 5, where a series of six oblique tows was made in order of progressively shallower depths between 78 m and the surface. The net was towed at the desired depth for 10–15 min, with the descent and ascent of the net done as quickly as possible to minimize contamination.

The inshore distribution of platycephalid larvae was assessed during ichthyoplankton sampling conducted in October, November and December 1996 at four stations in Norfolk Bay. Samples were collected with a 100 cm diameter ring net with 500 µm mesh. Each station consisted of a separate surface and oblique tow to a maximum depth of 15 m (bottom depth permitting) at a tow speed of ~3 knots. During inshore surveys, surface and bottom temperatures were recorded with a temperature/depth probe (±0.1°C, ±0.1 m). All other sampling protocols were the same as those described for shelf plankton sampling.

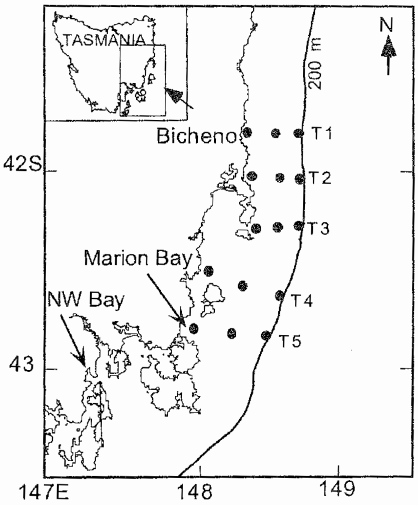


Fig. 2. Position of ichthyoplankton sampling stations on five transects (T1–T5) along the east coast of Tasmania. Shelfbreak is represented by the 200 m contour.

Laboratory procedures

Biological processing for all fish included fork length (FL) (to the nearest millimetre), total weight (to the nearest gram) and sex, gonad stage and gonad weight (to the nearest gram). Fish were sexed and their macroscopic gonadal stages determined according to the criteria described in Table 2.

Gonadosomatic index (GSI) was calculated from the formula:

$$\mathrm{GSI} = \frac{\text{gonad weight}}{\text{somatic weight}} \times 100$$

Platycephalid larvae were sorted from plankton samples in a rotatable sorting ring under a dissecting microscope. All unspecified body lengths refer to notochord length (NL) in preflexion and flexion larvae (tip of the snout to the posterior end of the notochord), and to standard length (SL) (i.e. tip of the snout to the posterior region of the hypural plate) in postflexion larvae and juveniles. All measurements are expressed as mean percentage of body length. Pre-anal length is defined as the horizontal distance from the tip of the snout to the anterior origin of the anal fin or anal-fin anlagen. Pectoral-fin length is defined as the distance from the pectoral-fin base to the posterior tip of the longest pectoral ray. Body depth at pectoral is equivalent to 'body depth' of Leis and Rennis (1983). Other definitions, such as body shape, follow Leis and Trnski (1989). Nomenclature of head spination follows that of Moser and Ahlstrom (1978). Larval measurements were made using an ocular micrometer and drawings made with the aid of a camera lucida.

Statistical analysis

Spatial and temporal variations in the abundance (N tow^{-1}) of small juvenile *P. bassensis* from beam trawling in Norfolk Bay were assessed by two-way analysis of variance (ANOVA) with habitat considered fixed and time a random factor. Analysis was restricted to fish <18.0 cm that were identified as representing the 0+ and 1+ cohorts from analysis of modal progression and ageing from sectioned

Table 2. Macroscopic staging criteria used for female and male *Platycephalus bassensis*

Stage	Category	Female	Male
1.	Virgin	Small strap with rounded edge, less than 3/4 length of body cavity. Pink, firm texture.	Flattened and ribbon like, less than 3/4 length of body cavity.
2.	Maturing virgins	Virgin: at least 3/4 of body length, pink and glassy Recovering: as long as body cavity, bloodshot and flabby at posterior.	Virgin: at least 3/4 length of body cavity, flattened and ribbon like. Recovering: as long as body cavity, slightly bloodshot and ribbon like.
3.	Developing	Almost length of body cavity, opaque and becoming yellow. Ova not discernible.	Almost length of body cavity, firm, larger and creamy pink.
4.	Late developing	Full length of body cavity, opaque and yellowish pink. Individual ova discrete.	Full length of body cavity, less firm and more rounded.
5.	Ripe	Full length of body cavity and swollen, occupying all available space. Ovary and ova becoming transparent.	Full length of body cavity and swollen, occupying all available space. Pinkish white and soft.
6.	Running ripe	Eggs express with slight pressure. Ovary pinkish, clear and granular.	Testes extrude milt with gentle pressure on belly. Very soft.
7.	Spent	Slack and bloodshot. Few residual oocytes present.	Testes broad, flaccid and bloodshot, little residual milt present.

sagittal otoliths (Jordan 1998). Data were tested for conformity to the assumptions of ANOVA by the F_{max} test for heteroscedascity and by examining normal probability plots. Transformation of abundance to $\ln(x+1)$ resulted in homogeneity of variances and distribution of residuals. Ryan's Q test was used to identify significant differences among means when there were significant main effects or interactions in the ANOVA. Ryan's Q test is considered to be the most powerful post-hoc test that allows the user to control experiment-wise error rate (Day and Quinn 1989). Calculations were performed with the Peritz program (Martin and Toothaker 1989).

Results

Gonadal development

Trends in monthly mean gonadosomatic index (GSI) showed the same overall trend for both male and female *P. bassensis* (Fig. 3). Mean female GSIs rose from minimum values in May to a peak in October in both years before declining through to low values by March. Mean male GSIs exhibited similar trends, although values decreased rapidly from October to November in 1996 before increasing again in December. This trend more likely reflects the absence of running ripe fish in November rather than indicating a period of reduced spawning activity in that month.

The temporal patterns of spawning from the GSIs is also reflected in the monthly trend in gonad stages, with all males and females in the resting phase (Stage 2) from April to June, and ripe, running ripe and spent fish (≥ Stage 5) present from October to March (Fig. 4). The decrease in GSIs from October to March reflects the increasing proportion of spent (Stage 7) and recovering (Stage 2) fish through these months and indicates that an increasing proportion of the population has completed spawning by January. Gonads reached a maximum of 10.2% and 18.7% of total body weight for males and females, respectively, during the spawning season.

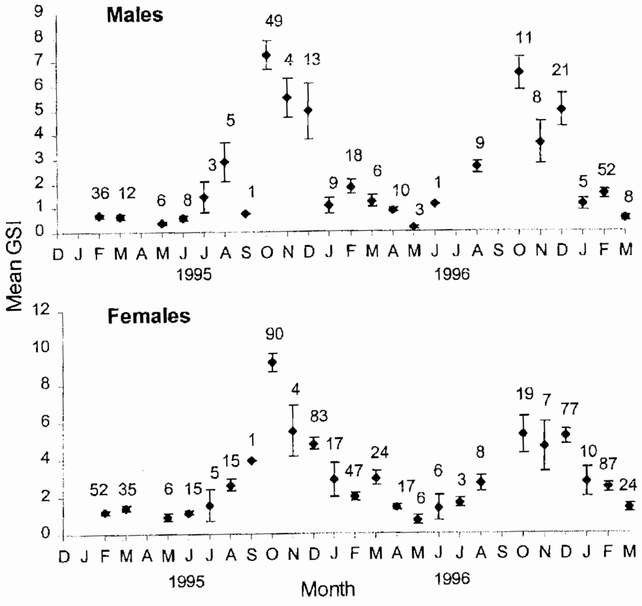


Fig. 3. Mean gonadosomatic indices (GSIs) for male and female *Platycephalus bassensis* caught inshore between February 1995 and February 1997. Error bars, s.e.

Larval development

Identification Identification of larvae to the family Platycephalidae was based on a combination of characters including a large and wide head with extensive spination, moderate to large, fan-shaped pectoral fins and the presence of 26–28 myomeres (Neira and Miskiewicz 1998). Identification to species using meristic characters is difficult as there are few differences between species (Table 3). Larvae were identified as those of *Platycephalus bassensis* by comparison with adult characters and distributions, timing of spawning and establishment of a developmental series.

Despite extensive sampling of shelf and inshore waters of southern and eastern Tasmania, no juvenile or adult specimens of *Neoplatycephalus aurimaculatus*, *P. speculator* and *P. laevigatus* have been recorded (Jordan 1997), and these species appear to be restricted to waters of Bass Strait and northern Tasmania. Whereas *N. richardsoni* are common on the shelf of southern and eastern Tasmania, spawning occurs during summer (December–March), with no evidence of spring spawning (Jordan 1997). A single series of platycephalid larvae was present in Norfolk Bay during the period of peak spawning activity of *P. bassensis* (Nov.), strongly suggesting that they are the larvae of *P. bassensis*. A second developmental series of platycephalid larvae was present in the eastern Tasmanian shelf samples taken in January 1989 and 1990, which was characterized by melanophores on the dorsal surface of the trunk in all stages and the presence of large teeth on the lower jaw and roof of the mouth in flexion and postflexion larvae. The presence of strong teeth is a diagnostic character of the genus *Neoplatycephalus* (Gomon *et al.* 1994), indicating that this second series was larvae of this genus.

Morphology Larvae of *Platycephalus bassensis* are pelagic. The smallest *P. bassensis* larvae examined (3.0 mm) had a functional mouth and coiled gut with yolk absorption complete. The head is small and compressed in preflexion larvae (HL = 24%), but becomes moderate during flexion (Table 4, Fig. 5*A*–*D*). The mouth is large, reaching to approximately the centre of the eye in all larval stages, whereas the snout increases in length and becomes flatter during flexion. There are no strong teeth on the roof of the mouth or lower jaw in any stage. A small gas bladder was inflated and visible above the foregut in preflexion and flexion larvae. The body depth is moderate (BD = 19–21%) with little change in body shape during larval development. Pectoral fins are moderate and fan-shaped increasing in size during flexion. Notochord flexion commences at 6.0 mm and is almost complete in the largest larvae examined (8.4 mm). Larvae have 27 myomeres (10~11+16~17).

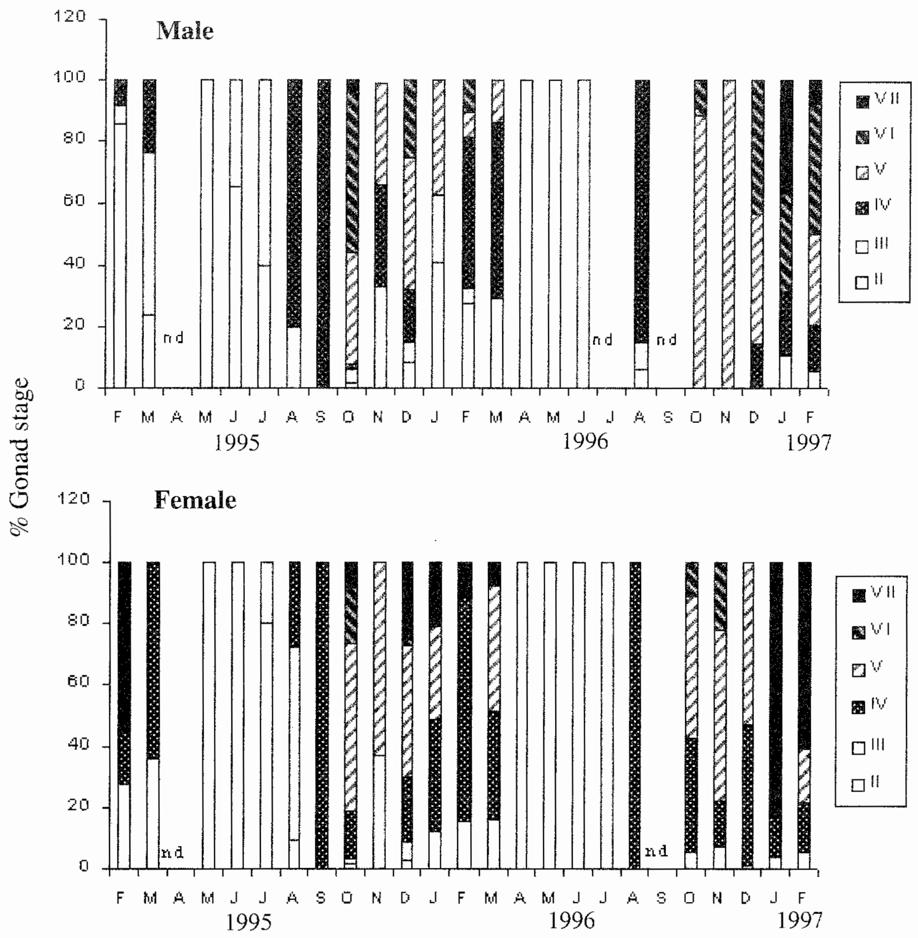


Fig. 4. Monthly gonad-stage percentages for male and female *Platycephalus bassensis* caught inshore between February 1995 and February 1997.

Fin development

Development of the pectoral fins is precocious with 1–2 incipient rays present in the smallest larvae examined (3.0 mm), ossification commencing in late preflexion larvae (5.4 mm) (Fig. 5). The pectorals have a full complement of 19–20 rays and reaching up to 17.5% of body length during flexion (7.4 mm). Pelvic fin buds are visible in 5.9–6.0 mm larvae as small swellings either side of the gut. The pelvics develop rapidly, having a full complement of I,5 rays by 8.4 mm. Anlagen of both anal and second dorsal fins appear early during flexion with distinct bases present by 7.0 mm. Incipient rays first appear by 7.4 mm with up to 12 rays ossified in the largest larva examined (8.4 mm). The first dorsal fin anlagen first appears by 7.4 mm with 5 spines ossified by 8.4 mm. The caudal fin anlagen first appears on the ventral surface of the notochord immediately prior to flexion (5.8 mm) with a total of 10 rays ossified by 8.4 mm.

Spination

One small anterior preopercular spine was present in the smallest larvae examined (3.0 mm), with two present by 3.5 mm (Fig. 5). A single posterior preopercular spine is present

Table 3. Meristic characters of platycephalid species present in Tasmanian waters

Collated from Gomon *et al.* (1994)

	Dorsal	Anal	Pectoral	Pelvic	Caudal	Vertebrae
Neoplatycephalus richardsoni	VIII–IX,14	14	19–20	I,5	15	–
Neoplatycephalus aurimaculatus	IX,14	14	16–20	I,5	15	–
Platycephalus bassensis	VIII–IX,14	14	19–20	I,5	15	27
Platycephalus speculator	VIII,14	14	19–21	I,5	15	27
Platycephalus laevigatus	IX,14–15	14–15	18–21	I,5	15	27

Table 4. Body proportions of *Platycephalus bassensis* larvae

Values are mean (+ s.d.) percentage of body length; *n*, no. individuals). Below dashed line: specimens undergoing notochord flexion

Size range (mm)	*n*	Pre-anal length	Body depth at pectoral	Head length	Pectoral-fin length
3.01-4.00	7	43.5 (3.5)	21.2 (2.8)	24.0 (1.3)	11.3 (0.9)
4.01-5.00	25	46.1 (3.0)	19.6 (0.9)	26.3 (1.7)	12.8 (1.1)
5.01-6.00	18	49.4 (2.0)	18.9 (0.4)	27.5 (1.5)	14.9 (1.0)
6.01-8.39	15	51.0 (1.4)	20.9 (1.4)	30.5 (1.8)	17.5 (0.9)

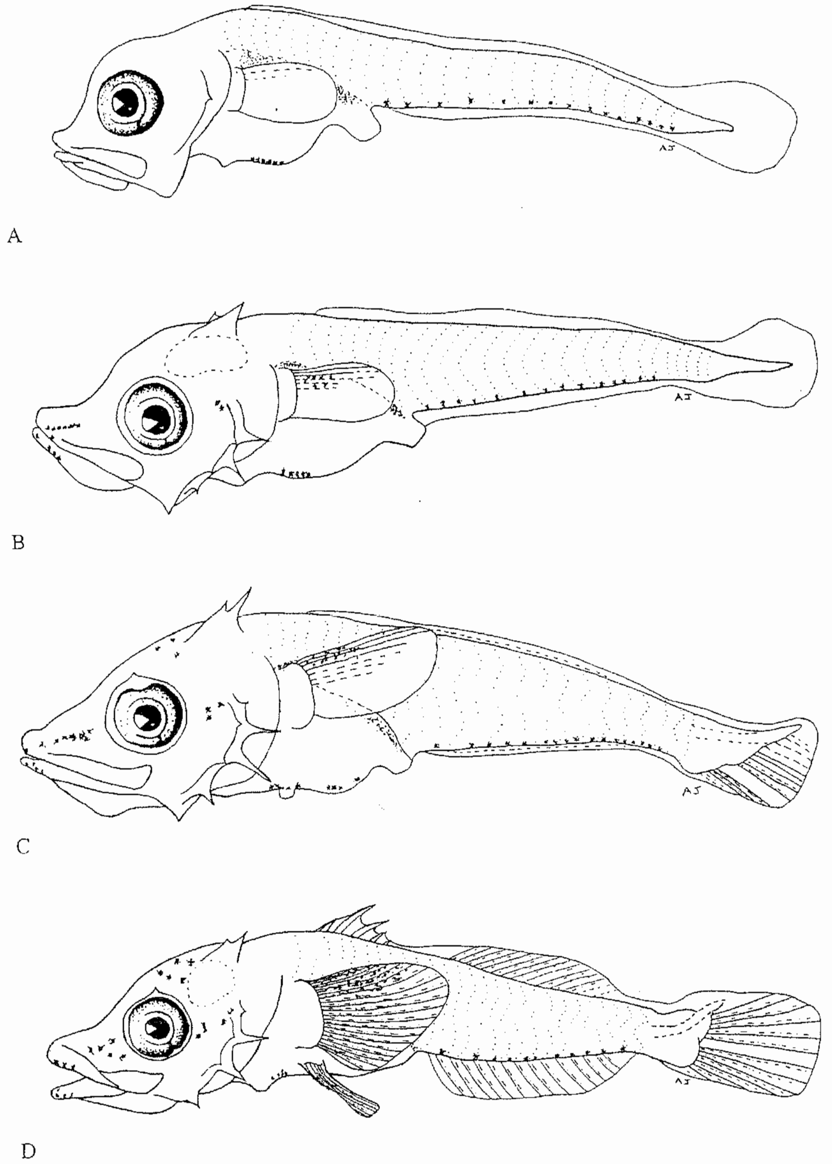


Fig. 5. Developmental stages of *Platycephalus bassensis* larvae: *(A)* 3.0 mm, *(B)* 5.7 mm, *(C)* 7.1 mm and *(D)* 8.4 mm.

by 3.5 mm, increasing to four immediately prior to flexion (5.9 mm), with the second and third spines becoming the longest. A single parietal spine develops at about 4.0 mm, with a further small spine appearing on the anterior portion of the spine by 5.1 mm. A small supraocular spine is visible by 5.8 mm and remains small after settlement.

Pigmentation

Pigment appears at the tip of the upper and lower jaws and snout by 3.5 mm and remains moderate during flexion (Fig. 5). Several scattered melanophores appear on the preopercle by 5.2 mm and on the dorsal surface of the head by about 5.9 mm. A single row of 13–17 melanophores is present on the ventral surface of the tail and 5–9 small melanophores on the ventral surface of the gut in all larval stages. Numerous small melanophores are present on the posterior portion of the gut in preflexion larvae, increasing in number during flexion. Pigment on the pectoral fin appears in early preflexion larvae and is restricted to the upper fin rays, with the lower rays remaining unpigmented. Internal pigment is present on the dorsal surface of the gas bladder during all larval stages.

Larval distribution and hydrography

Platycephalus bassensis larvae were caught in both early and late January of 1989 and 1990 on the shelf of eastern Tasmania (Fig. 6). Highest larval densities occurred almost exclusively at inshore stations on all transects in both years, with maximum densities of 14 larvae 200 m^{-3} at the inshore station on Transect 4 in late January 1989. Over both years, approximately 79% of larvae were caught at inshore stations, 21% at mid-shelf stations, with no larvae at shelf-break stations. Larvae in late January 1989 were vertically stratified in the water column with highest densities occurring at 20–30 m, just above the thermocline (Fig. 7). The overestimate of abundances at depth due to contamination is expected to be minimal due to the small proportion of time that the net sampled the non-targeted depths. The thermal stratification reflects the presence of warm East Australian Current (EAC) water (characterized by the 17°C isotherm) and cooler bottom water, forming a shallow (~30 m) mixed layer.

Sea-surface temperatures on the shelf of eastern Tasmania during January of 1989 and 1990 reflected both the presence of warm EAC water of northerly origin and cooler southerly water (Fig. 6). In early January 1989, there was evidence of an influx of warm EAC water over the shelf-break from the north-east with warmest water on the outer shelf (Fig. 6*A*). This pattern continued in late January 1989, with EAC water evident over most of the shelf, resulting in an onshore flow of water. In early January 1990 the shelf was dominated by cooler water of southerly origin, whereas by late January there was evidence of warmer EAC water moving across the shelf from the north-east (Fig. 6*B*).

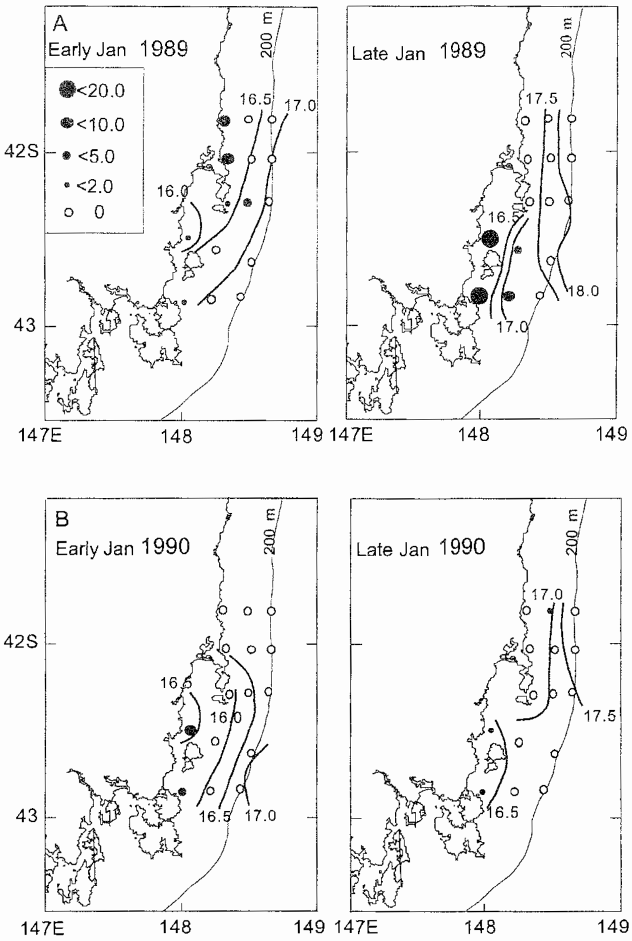


Fig. 6. *Platycephalus bassensis* larval concentrations (*N* per 200 m^{-3}) and sea-surface temperatures (°C) during early and late January of *(A)* 1989 and *(B)* 1990 on the shelf of eastern Tasmania.

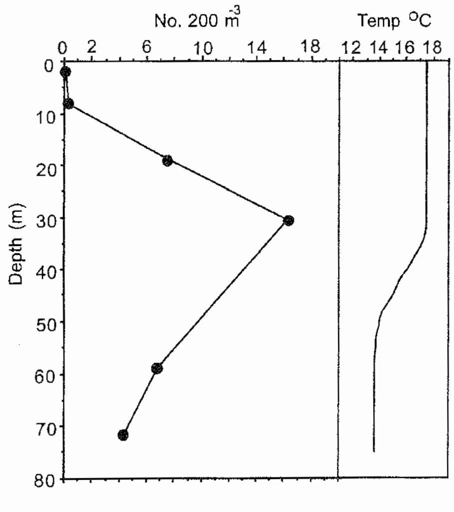


Fig. 7. Vertical distribution of *Platycephalus bassensis* larvae at the mid-shelf station on Transect 5 in late January 1989.

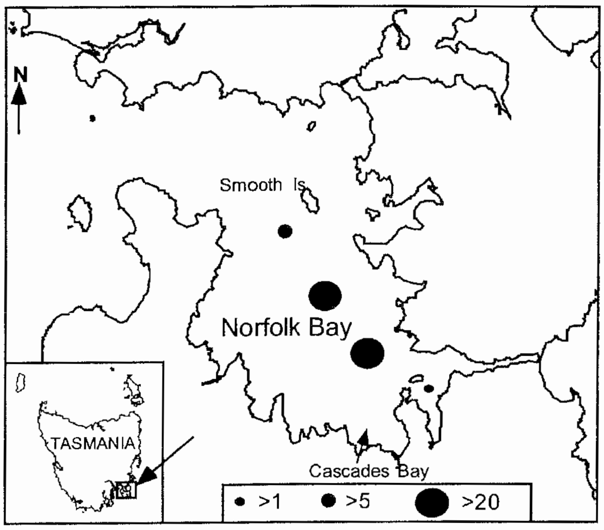


Fig. 8. *Platycephalus bassensis* larval concentrations (*N* per 200 m^{-3}) in Norfolk Bay in November 1996.

Despite monthly sampling in Norfolk Bay during the three months of peak spawning activity (Oct.–Dec.), *P. bassensis* larvae were only caught in November. At that time, larvae were present at all four stations, although densities were highest in the middle of the bay, peaking at 35 larvae 200 m^{-3} (Fig. 8). All *P. bassensis* larvae were caught in oblique tows with no larvae caught in surface tows in any month.

Settlement

Size compositions of juvenile *P. bassensis* are dominated by a single cohort from February to December 1996, although in some months there was evidence of bimodal distribution within this cohort (Fig. 9). This cohort had a mean length of 6.2 cm in February 1996 and represents 0+ fish from spawning that took place the previous spring and summer. The broad range of lengths present in most months indicates that settlement occurred over an extended period. The earliest month settlement was recorded was January 1997, although the large range in lengths (2.3–7.4 cm) suggests that settlement had begun some time earlier.

Abundance of 0+ and 1+ *P. bassensis* in Norfolk Bay was significantly higher in unvegetated compared with *Heterozostera* habitats ($P<0.001$) (Fig. 10). Post-hoc tests revealed that this pattern was consistent in all sample dates except February, April and August 1995 when abundances were low in both habitats (Ryans Q-test; $P<0.05$).

Discussion

Gonadal development

The presence of ripe, running ripe and spent *P. bassensis* ($\geq$ Stage 5) from October to March clearly demonstrates that in southern and eastern Tasmania, spawning occurs over an

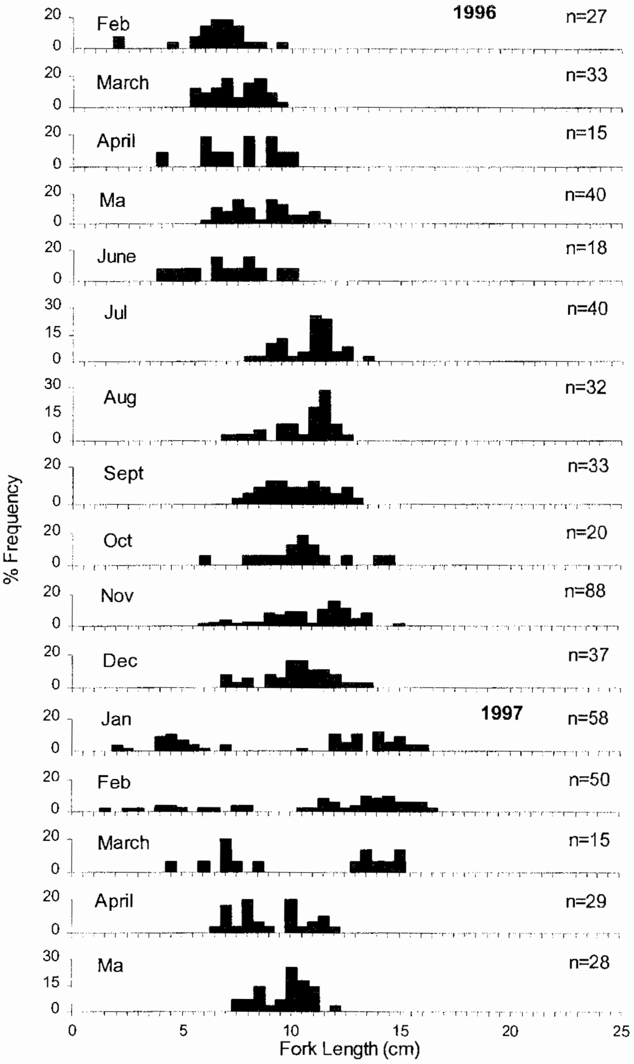


Fig. 9. Length–frequency distributions of juvenile *Platycephalus bassensis* from eastern and southern Tasmania between February 1996 and May 1997; *n*, sample size.

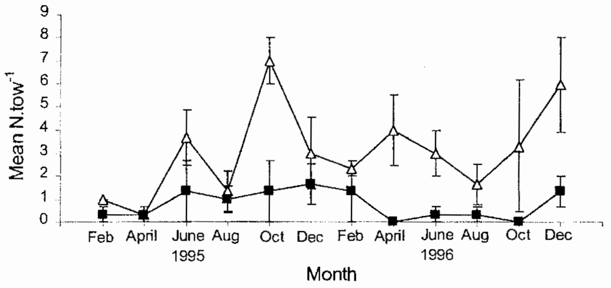


Fig. 10. Mean abundance (*N* tow^{-1}) of 0+ and 1+ *Platycephalus bassensis* collected by beam trawl from (■) *Heterozostera tasmanica* and (△) unvegetated habitats in Norfolk Bay between February 1995 and December 1996.

extended period lasting up to six months. The increasing proportion of fish with resting stage gonads from January to March indicates, however, that the bulk of spawning occurs between October and December, with a lower level of spawning activity in the latter half of the spawning period. This is also reflected in the fact that the highest GSIs occur between October and December. Spawning commenced soon after water temperature rose in October, suggesting that this may be linked to the timing of the spring bloom in productivity in these waters, which begins around mid-September (Harris *et al.* 1987).

In contrast, the pattern in monthly GSIs of *P. bassensis* in Port Phillip Bay indicated that spawning occurred between August and October, with ripe fish caught as late as December thought to have reabsorbed their gonads (Brown 1978). There are several possible reasons to explain the differences in the duration of the spawning season. Firstly, Brown (1978) suggested that spawning in *P. bassensis* in Port Phillip Bay is restricted to spring months to reduce competition with the other sympatric species, *P. fuscus* and *P. speculator*, that spawn in the bay from November to February. As *P. bassensis* is the only abundant platycephalid in coastal waters of southern and eastern Tasmanian, such sympatric competition is not evident. Variations in the spawning duration may also be related to differences in the seasonal cycle in water temperature with spawning in Port Phillip Bay occurring between 10.5^{o} and 17.0^{o}C (Brown 1978). Although spawning in coastal waters of Tasmania occurred between 10.5^{o}C and 17.4^{o}C, maximum temperatures occurred late in the spawning period (Feb.).

The extended spawning period for *P. bassensis* in Tasmania may also be in response to the highly variable cycles in productivity that occur in these waters. Spring blooms occur primarily between September and November, although the duration of the bloom can vary by as much as three months from year to year, with periods of increased westerly winds resulting in an increase in primary production right through the summer period (Harris *et al.* 1991). The extended spring and summer spawning of *P. bassensis* may therefore reflect a strategy to maximize the number of larvae encountering suitable feeding conditions.

The presence of running ripe and spent male and female *P. bassensis* in all estuarine (Georges Bay), coastal (Prosser Bay and Norfolk Bay) and shelf areas sampled confirms that spawning occurs throughout their range in southern and eastern Tasmania. This is further supported by the presence of small preflexion larvae in Norfolk Bay and on the inner shelf. Whereas temperate platycephalid species have been found to spawn in estuaries (Hyndes *et al.* 1992) and coastal embayments (Brown 1978), shelf spawning has not been previously identified, particularly in *P. bassensis*.

Larval development

Development of larvae of *P. bassensis* is similar to that described for other platycephalid larvae off southern Australia, *P. speculator* (Hyndes *et al.* 1992) and *P. fuscus* (Neira and Miskiewicz 1998). These species are characterized by a large, wide head with extensive spination, moderate to large fan-shaped pectoral fins and 26–28 myomeres. Larvae of *P. bassensis* are distinguished from both *P. fuscus* and *P. speculator* by the larger size at both notochord flexion (6.0–>8.4 mm) and pelvic (5.9–7.4 mm) and dorsal fin (6.2–>8.4 mm) formation. In addition, the trunk and tail are only lightly pigmented in *P. bassensis* larvae, which contrasts with moderate to heavy pigment in larval *P. fuscus* and *P. speculator* (Neira and Miskiewicz 1998).

Small platycephalid larvae can be confused with scorpaenids and triglids that also have early developing fan-shaped pectoral fins and extensive spination. Triglid larvae, however, have more prominent post-temporal spines, a duck-bill-shaped snout, 27–37 myomeres and lower two or three pectoral fin rays elongate and detached from the rest of the fin in larger larvae (Jordan *et al.* 1998). Small scorpaenid larvae have a rounder head without a flattened, elongate snout, and larger larvae are easily distinguished by morphology, fin meristics and the presence of a single dorsal fin (Neira and Furlani 1998).

Larval distribution

The fact that *P. bassensis* larvae were most abundant at inshore stations in both 1989 and 1990 suggests that shelf spawning in eastern Tasmania is concentrated on the inner-shelf. This is supported by the higher abundances of mature *P. bassensis* on the inner-shelf of the east coast during summer and their absence from outer-shelf waters (Jordan 1998). This conclusion, however, will be influenced by the hydrography and resultant transport of larvae from the spawning area. The oceanography of these waters during the spawning season is determined by a combination of the local westerly wind stress, and large scale oceanographic circulation dominated by the warm, stratified East Australian Current (EAC) water, and cool, well mixed water of subantarctic origin (Harris *et al.* 1987).

During January 1989, the shelf of eastern Tasmania was dominated by subtropical EAC water resulting in an upper mixed layer (~40 m) of EAC water that originated offshore and moved across the entire shelf, resulting in an onshore flow of waters down to around 40 m. Hence, the concentration of *P. bassensis* larvae at inshore stations in January 1989 may reflect strong onshore transport in that year. A similar inshore distribution was evident in eggs and larvae of jack mackerel (*Trachurus declivis*) in eastern Tasmania in January 1989, this being attributed to a strong onshore flow of EAC water across the shelf (Jordan *et al.* 1995). Warmer sea-surface temperatures were also present in January 1990, although the EAC water was mainly restricted to the outer-shelf, with cooler waters dominating inshore. Therefore, the fact that *P. bassensis* larvae were concentrated inshore in January 1990 during a period of reduced EAC influence and onshore flow suggests that shelf spawning is concentrated on the inner-shelf and larvae are retained inshore by subsurface currents. Although these currents are predominantly alongshore during spring and summer, cross-shelf currents are present and are mainly onshore during this period (Freeland *et al.* 1985). In contrast, there is a consistent pattern of offshore flow of surface waters suggested by the movements of satellite-tracked drifter buoys (Cresswell *et al.* 1994), although patterns of drifter movement during years of reduced westerly wind stress and increased EAC influence have not been documented.

The suggestion that the distributional patterns of *P. bassensis* larvae are influenced by the subsurface currents on the shelf is further supported by the concentration of larvae in mid-water. This is consistent with platycephalid larvae on the inner-shelf of New South Wales where larvae were concentrated in mid-water (15–30 m) and their vertical distribution was independent of the depth stratified layer, suggesting that larval behaviour was the major influence determining the vertical distribution (Gray *et al.* 1992; Gray 1996). Therefore, despite the lack of data on the vertical distribution of larvae during non-stratified conditions in the present study, the distribution observed in January 1989 may also reflect that during non-stratified periods. This is consistent with the presence of larvae exclusively in oblique tows in Norfolk Bay. This strategy would act to minimize the advective loss of larvae to offshore waters during periods of increased westerlies and offshore flow of surface waters.

Such variations in larval transport have been identified as a significant source of mortality (Nelson *et al.* 1977). The offshore transport of eggs and larvae in species whose larvae are distributed inshore and whose nursery areas are also inshore can play a major role in determining recruitment success (Bailey 1981). Such offshore advective losses of *P. bassensis* larvae spawned in coastal embayments and estuaries are unlikely as there was no evidence of large scale replacement of coastal waters that would transport larvae away from their shallow coastal settlement habitat (Jordan 1998). The concentration of shelf spawning on the inner-shelf region may also act to reduce offshore Ekman transport as such movement is often minimal directly adjacent to the coast (Parrish *et al.* 1981). This is supported in the present study by the concentration of larvae on the inner-shelf in 1990, despite increased westerly wind stress in that year.

Settlement

The size-class of juvenile *P. bassensis* present between February and December 1996 represents the 0+ age-class resulting from spawning that commenced the previous October. The broad range of lengths in every month indicates that settlement occurred over an extended period reflecting the protracted spawning period of *P. bassensis*. Newly settled individuals were first caught in January, although the presence of fish up to 7 cm in that month suggests that settlement had begun some time earlier. The smallest settled individual (2.1 cm) did not have fully transformed juvenile morphology and pigmentation, indicating that settlement to benthic habitats occurs close to this size. This is larger than the size at settlement of approximately 1.3 cm in *P. speculator* (Hyndes *et al.* 1992). The small number of newly settled *P. bassensis* caught in the present study is likely to reflect escapement under the ground line of the beam trawl rather than an ontogenetic shift in habitat preference, as initial settlement occurs exclusively into subtidal unvegetated habitats.

Abundance of juvenile *P. bassensis* was consistently higher in unvegetated compared with *Heterozostera* habitats, indicating that the unvegetated subtidal zone is the primary nursery area for the species. This is supported by the low abundance of *P. bassensis* in shallow beach habitats during extensive beach seine surveys of Tasmania (Last 1983; Jordan 1998) and is consistent with the preference for unvegetated habitats in Western Port, Vic. (Edgar and Shaw 1995). There is also evidence that inner- and mid-shelf regions of southern and eastern Tasmania are not an important nursery area for *P. bassensis* (Jordan 1998). It is likely that *P. bassensis* use unvegetated habitats as a nursery area as camouflage allows some protection from predators. Similar recruitment to unvegetated habitats is common in families such as Pleuronectidae (flounders) that are also protected by camouflage (Connolly 1994; Jenkins *et al.* 1997). Some studies have also identified a preference for unvegetated habitats in juvenile platycephalids (Hyndes *et al.* 1992; Ayvazian and Hyndes 1995; Edgar and Shaw 1995). The significance of unvegetated habitats as a nursery area for temperate Australian platycephalids is also supported by the lack of juveniles in vegetated habitats, despite extensive surveys of both seagrass (Burchmore *et al.* 1984; Bell and Westoby 1986) and reef-algal beds (Jenkins and Wheatley 1997). Although seagrass beds are widely recognized as an important nursery area due to high food resources (Bell and Pollard 1989; Edgar *et al.* 1994), enhanced food production in shallow unvegetated habitats can occur due to the presence of detached macrophytes (Robertson and Lenanton 1984) and regular phytoplankton blooms (McLachlan *et al.* 1981).

Of particular interest is the absence of juvenile *Neoplatycephalus richardsoni* from shallow habitats in the present study, despite the presence of spawning fish (Jordan 1997) and larvae (Jordan, unpublished) in adjacent shelf waters. Little is known of the distribution of nursery areas of *N. richardsoni*, with few small juveniles caught on the shelf, leading to the presumption that juveniles inhabit shallow inshore nursery areas (Jordan 1997). Either discrete nursery areas occur outside southern and eastern Tasmanian shelf waters, the abundance of juvenile *N. richardsoni* was low during the study period, or they possibly remain as pelagic post-larvae for an extended period as they are one of the few platycephalids that retain their swim bladder (Gomon *et al.* 1994).

Size compositions of 0+ *P. bassensis* indicate the presence of several cohorts in most months. The existence of multiple 0+ cohorts may reflect periodicity in the temporal pattern of spawning (Szedlmayer *et al.* 1990; Jordan 1994), variability in larval supply (Jenkins and Black 1994) and larval duration (Cowen 1991; Jenkins and May 1994), or a combination of factors. The monthly distribution of GSIs in *P. bassensis* shows no indication of distinct peaks in spawning, although such monthly sampling may miss finer temporal patterns. Variations in larval supply of *P. bassensis* through periodicities in anomalous transport are also unlikely to result in variations in settlement because extensive settlement habitat is present close to or within the area of spawning (Jordan 1998).

The presence of several cohorts of *P. bassensis* may also reflect periodicity in larval survival through short-term variations in zooplankton production that are common in these waters (Harris *et al.* 1991). This is supported by the absence of larvae in Norfolk Bay in October and December despite the presence of spawning and spent fish in the bay in those months. Such periodicity in plankton blooms has been strongly correlated with peaks in recruitment of larvae in south-eastern Tasmania, with a match/mismatch hypothesis used to explain variations in larval survival (Thresher *et al.* 1989). There is also evidence to suggest that increased westerly wind stress resulting in high levels of zooplankton production that persist through the spring and summer spawning period of *P. bassensis* results in strong recruitment of that year-class (Jordan 1998). Further studies examining the temporal patterns of larval and zooplankton production will be required before the influence of variations in food availability on larval survival and subsequent recruitment in *P. bassensis*, and other commercially important coastal fish species in this region, can be fully evaluated.

Acknowledgments

Thanks to the many staff of the Marine Research Laboratories for their assistance in the field and laboratory, and to Robert White, Jeremy Lyle and two referees for providing comments on the manuscript. This research was supported by grants DFT2Z and 94/037 from the Fisheries Research and Development Corporation.

References

Ayvazian, S. G., and Hyndes, G. A. (1995). Surf zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? *Marine Biology* **122**, 527–36.

Bailey, K. M. (1981). Larval transport and recruitment of Pacific Hake *Merluccius productus*. *Marine Ecology Progress Series* **6**, 1–9.

Bell, J. D., and Pollard, D. A. (1989). Ecology of fish assemblages and fisheries associated with seagrasses. In 'Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region'. (Eds A. W. D. Larkum, A. J. McCoomb and S. Shepherd.) pp. 565–609. (Elsevier: Amsterdam.)

Bell, J. D., and Westoby, M. (1986). Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. *Journal of Experimental Marine Biology and Ecology* **104**, 249–74.

Brown, I. W. (1978). Ecology of three sympatric flatheads (Platycephalidae) in Port Phillip Bay, Victoria. Ph.D. Thesis, Monash University, Victoria.

Burchmore, J. J., Bell, J. D., and Pollard, D. A. (1984). Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New South Wales. *Aquatic Botany* **18**, 71–87.

Connolly, R. M. (1994). A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. *Australian Journal of Marine and Freshwater Research* **45**, 1033–44.

Cowen, R. K. (1991). Variation in the planktonic larval duration of the temperate wrasse *Semicosyphus pulcher*. *Marine Ecology Progress Series* **69**, 9–15.

Cresswell, G., Wells, G., and Peterson, J. (1994). Australian satellite-tracked drifters 1991–1994. Report to Fisheries Research and Development Corporation (FRDC). (CSIRO Division of Oceanography: Hobart, Tas.)

Day, R. W., and Quinn, G. P. (1989). Comparison of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**, 433–63.

Edgar, G. J., and Shaw, C. (1995). The production and trophic ecology of shallow-water fish assemblages in southern Australia. I. Species richness, size structure and production of fishes in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* **194**, 53–81.

Edgar, G. J., Shaw, C., Watson, G. F., and Hammond, L. S. (1994). Comparison of species richness, size structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* **176**, 201–26.

Fairbridge, W. S. (1951). The New South Wales tiger flathead, *Neoplatycephalus macrodon* (Ogilby). I. Biology and age determination. *Australian Journal of Marine and Freshwater Research* **2**, 117–78.

Freeland, H. J., Church, J. A., Smith, R. L., and Boland, F. M. (1985). Current meter data from the Australian Coastal Experiment and Data Report. CSIRO Marine Laboratories Report No. 169. 51 pp.

Gomon, M. F., Glover, J. C. M., and Kuiter, R. H. (1994). 'The fishes of Australia's south coast'. (State Print: Adelaide, SA.)

Gray, C. A. (1996). Do thermoclines explain the vertical distribution of larval fishes in the dynamic coastal waters of south-eastern Australia? *Marine and Freshwater Research* **47**, 183–90.

Gray, C. A., Otway, N. M., Laurenson, F. A., Miskiewicz, A. G., and Pethebridge, R. L. (1992). Distribution and abundance of marine fish larvae in relation to effluent plumes from sewage outfalls and depth of water. *Marine Biology* **113**, 549–59.

Gray, C. A., McElligott, D. J., and Chick, R. C. (1996). Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Marine and Freshwater Research* **47**, 723–35.

Harris, G. P., Nilsson, C., Clementson, L. A., and Thomas, D. (1987). The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. *Australian Journal of Marine and Freshwater Research* **38**, 569–90.

Harris, G. P., Griffiths, F. B., Clementson, L. A., Lyne, V., and Van der Doe, H. (1991). Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. *Journal of Plankton Research* **13** Suppl., 109–31.

Hyndes, G. A., Neira, F. J., and Potter, I. C. (1992). Reproductive biology and early life history of the marine teleost *Platycephalus speculator* Klunzinger (Platycephalidae) in a temperate Australian estuary. *Journal of Fish Biology* **40**, 859–74.

Jenkins, G. P. (1986). Composition, seasonality and distribution of ichthyoplankton in Port Phillip Bay, Victoria. *Australian Journal of Marine and Freshwater Research* **37**, 507–20.

Jenkins, G. P., and Black, K. P. (1994). Temporal variability in settlement of a coastal fish, the King George whiting, *Sillaginodes punctata*, is determined by low-frequency hydrodynamics. *Limnology and Oceanography* **39**, 1744–54.

Jenkins, G. P., and May, H. M. A. (1994). Variation in settlement and larval duration of King George whiting, *Sillaginodes punctata* (Sillaginidae), in Swan Bay, Victoria, Australia. *Bulletin of Marine Science* **54**, 281–96.

Jenkins, G. P., and Wheatley, M. J. (1997). The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *Journal of Experimental Marine Biology and Ecology* **221**, 147–72.

Jenkins, G. P., May, H. A., Wheatley, M. J., and Holloway, M. G. (1997). Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. *Estuarine and Coastal Shelf Science* **44**, 569–88.

Jordan, A. R. (1994). Age, growth and back-calculated birthdate distributions of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from eastern Tasmanian coastal waters. *Australian Journal of Marine and Freshwater Research* **45**, 19–33.

Jordan, A. R. (1997). Demersal trawl surveys of the continental shelf of southern and eastern Tasmania 1993–95. Technical Report of the Marine Laboratories Marine Research Division Tasmania No. **50**, 148 pp.

Jordan, A. R. (1998). The life-history ecology of *Platycephalus bassensis* and *Nemadactylus macropterus*. Ph.D. Thesis, University of Tasmania, Hobart, Australia. 191 pp.

Jordan, A. R., Pullen, G., Marshall, J. A., and Williams, H. (1995). Temporal and spatial patterns of spawning in jack mackerel, *Trachurus declivis* (Pisces: Carangidae), during 1988–91 in eastern Tasmanian waters. *Marine and Freshwater Research* **46**, 831–42.

Jordan, A. R., Richards, W., and Neira, F. J. (1998). Family: Triglidae. In 'The larvae of temperate Australian fishes: a laboratory guide for larval fish identification'. (Eds F. J. Neira, A. G. Miskiewicz and T. Trnski.) pp. 150–63. (University of Western Australian Press: Nedlands, WA.)

Kailola, P. J., Williams, M. J., Stewart, P. C., Reichelt, R. E., McNee, A., and Grieve, C. (1993). 'Australian Fisheries Resources'. (Bureau of Resources Sciences and Fisheries Research and Development Corporation: Canberra.) 422 pp.

Kojima, J. (1988). Platycephalidae. In 'An atlas of the early stages of fishes in Japan'. pp. 822–29. (Tokai University Press: Tokyo.) (In Japanese.)

Last, P. (1983). Aspects of the ecology and zoogeography of fishes from soft-bottom habitats of the Tasmanian shore zone. Ph.D. Thesis, University of Tasmania, Hobart, Australia.

Leis, J. M. and Rennis, D. S. (1983). 'The larvae of Indo-Pacific coral reef fishes.' (University of New South Wales Press: Sydney.) 269 pp.

Leis, J. M., and Trnski, T. (1989). 'The larvae of Indo-Pacific shorefishes.' (University of New South Wales Press: Sydney.) 371 pp.

Lyle, J. M., and Jordan, A. R. (1998). Tasmanian Scalefish Fishery Assessment – 1998. Fishery Assessment Report of the Tasmanian Aquaculture and Fisheries Institute. 98 pp.

Martin, S. A., and Toothaker, L. E. (1989). PERITZ: a FORTRAN program for performing multiple comparisons of means using the Peritz Q method. *Behaviour Research Methods, Instruments and Computers* **21**, 465–72.

McLachlan, A., Erasmus, T., Dye, A. H., Wooldridge, T., vander Horst, G., Rossouw, G., Lasiak, T. A., and McGynne, L. (1981). Sand beach energetics: an ecosystem approach towards a high energy interface. *Estuarine Coastal Shelf Science* **13**, 11–25.

Moser, H. G., and Ahlstrom, E. H. (1978). Larvae and pelagic juveniles of blackgill rock-fish, *Sebastes melanostomus*, taken in midwater trawls off Southern California and Baja California. *Journal of the Fisheries Research Board of Canada* **35**, 981–96

Neira, F. J. and Furlani, D. (1998). Family: Scorpaenidae. In 'The larvae of temperate Australian fishes: a laboratory guide for larval fish identification'. (Eds F. J. Neira, A. G. Miskiewicz and T. Trnski.) pp. 140–9. (University of Western Australia Press: Nedlands, WA.)

Neira, F. J., and Miskiewicz, T. (1998). Family: Platycephalidae. In 'The larvae of temperate Australian fishes: a laboratory guide for larval fish identification'. (Eds F. J. Neira, A. G. Miskiewicz and T. Trnski.) pp. 134–9. (University of Western Australia Press: Nedlands, WA.)

Neira, F. J., Coutin, P. C., and Elliot-Tippet, D. (1997). Commercial catches of selected scalefish species from Victorian waters, 1978–1995. Marine and Freshwater Resources Institute Report No. 2, 64 pp.

Nelson, W. R., Ingham, M. C., and Schaaf, W. E. (1977). Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. *Fishery Bulletin (US)* **75**, 23–41.

Parrish, R. H., Nelson, C. S., and Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography* **1**, 175–203.

Robertson, A. I., and Lenanton, R. C. J. (1984). Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. *Journal of Experimental Marine Biology and Ecology* **84**, 265–83.

Shaw, M., and Jenkins, G. P. (1992). Spatial variation in feeding, prey distribution and food limitation of juvenile flounder, *Rhombosolea tapirina* Guenther. *Journal of Experimental Marine Biology and Ecology* **165**, 1–21.

Szedlmayer, S. T., Weinstein, M. P., and Musick, J. A. (1990). Differential growth among cohorts of age-0 weakfish *Cynoscion regalis* in Chesapeake Bay. *Fishery Bulletin (US)* **88**, 745–52.

Thresher, R. E., Harris, G. P., Gunn, J. S., and Clementson, L. A. (1989). Phytoplankton production pulses and episodic settlement of a temperate marine fish. *Nature* **341**, 641–3.

Manuscript received 5 November 1999; revised and accepted 24 February 2000

Mar. Freshwater Res., 2001, **52**, 603–10

Larval distribution of blue grenadier (*Macruronus novaezelandiae* Hector) in south-eastern Australia: further evidence for a second spawning area

Barry D. Bruce, Scott A. Condie and Caroline A. Sutton

CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia. email: Barry.Bruce@marine.csiro.au

Abstract. Small numbers of blue grenadier, *Macruronus novaezelandiae*, larvae were found in coastal waters off eastern Victoria and southern New South Wales in August 1993. This is the first record of larval blue grenadier from mainland Australian waters. It is considerably further north than previous records of larvae and remote from the single known spawning ground off western Tasmania. Larvae were aged between 17 and 36 days and were largely confined to an inshore northward flowing water mass. Back calculated spawning dates indicated that larvae from eastern Victoria/southern NSW were spawned earlier than larvae collected during the same period off western and southern Tasmania. Otolith increment widths were significantly wider in larvae caught in eastern Victoria/southern NSW suggesting that they experienced faster growth and development conditions than the Tasmanian larvae. Three-dimensional modelling of circulation and particle advection suggested that the source of eastern Victoria/southern NSW larvae was most likely eastern Bass Strait. These data suggest that there is a second, albeit limited, spawning area for blue grenadier in south-eastern Australia.

Introduction

The blue grenadier, *Macruronus novaezelandiae*, is a large, southern temperate gadoid that supports commercial trawl fisheries in both Australia and New Zealand (Gunn *et al.* 1989). In Australian waters, blue grenadier are thought to be a single stock that is genetically distinct from New Zealand stocks (Kailola *et al.* 1993). This is supported by *(i)* the existence of a single known spawning ground for the species off western Tasmania (Gunn *et al.* 1989), *(ii)* the presence of coastal currents able to transport larvae from west-coast spawning grounds to nursery areas on the east coast of Tasmania (Thresher *et al.* 1989; Lyne and Thresher 1995) and *(iii)* a general pattern of genetic homogeneity (Milton and Shacklee 1987). However, some data regarding stock structure of blue grenadier in southern Australia are more ambiguous. Milton and Shacklee (1987) also noted that although there was no overall genetic pattern to suggest geographically distinct populations, there was a high degree of microspatial heterogeneity. They suggested that this might be due to the existence of two or more stocks of blue grenadier overlapping in time and space. A preliminary examination of long-lived endoparasites by Lester (reported in Milton and Shacklee 1987) also did not support the concept of extensive movement of blue grenadier between east and west coasts of Tasmania.

Although only a single spawning ground for blue grenadier has been located in southern Australia, the occurrence of multiple spawning areas would be consistent with the species' behaviour in New Zealand. Blue grenadier (= hoki) spawn in two main areas in New Zealand: off the Westland region of the South Island, and in Cook Strait (Murdoch and Chapman 1989; Livingston 1990; Zeldis *et al.* 1998). Blue grenadier from these two spawning areas are considered to be different stocks (Livingston and Schofield 1996) and this has led to the establishment of separate management zones between east and west coasts (Livingston 1990; Annala 1995).

A second spawning ground for blue grenadier in Australian waters was suggested by Thresher *et al.* (1988) on the basis of their collection of small numbers of small larvae from north-eastern Tasmania. Subsequent intensive sampling, however, failed to find any further concentrations of blue grenadier larvae either in that area or outside Tasmanian waters, leading to the conclusion that if spawning did occur off north-eastern Tasmania, it was both minor and intermittent (Gunn *et al.* 1989). There are also persistent (but unconfirmed) reports of ripe blue grenadier in areas other than western Tasmanian waters (e.g. western Victoria and eastern Bass Strait) and juveniles (<20 cm) are sometimes reported from eastern Victoria and southern New South Wales (J. Garvey, Bureau of Resource Sciences, Canberra, personal communication; CSIRO unpublished). These reports suggest that some level of spawning may occur in areas of southern Australia other than the west coast of Tasmania, despite there being no reports by commercial fishers of blue grenadier aggregations outside the western Tasmanian spawning ground.

We report herein the first discovery of blue grenadier larvae from southern New South Wales (NSW) and eastern

10.1071/MF99171 1323-1650/01/040603

Victoria (Vic.). These data, combined with the output from a new advection model, further support the existence of a second spawning area for blue grenadier in eastern Bass Strait.

Materials and methods

Sampling procedures and laboratory details

Larvae were sorted from ichthyoplankton samples collected on five transects spaced roughly equidistantly between Bermagui (NSW) and Pt Hicks (Vic.), a series of additional stations in shelf waters in the vicinity of Eden (NSW) and stations along the west and south coasts of Tasmania (Fig. 1). Sampling was designed to study the distribution of larvae of commercial fin-fish species in south-eastern Australian waters (Bruce *et al.* 1996). Each transect consisted of four stations (nearshore, 40–50 m bottom depth), midshelf (100–120 m), shelf edge (180–200 m) and offshore (10 nautical miles seaward of the shelf edge). Sampling in Tasmanian waters targeted mid-shelf locations where previous sampling had recorded large numbers of blue grenadier larvae (Thresher *et al.* 1988). Samples were collected from RV *Southern Surveyor* between 16 and 25 August 1993. Stations were occupied on arrival, regardless of the time of day. At each station, temperature and salinity profiles were recorded with a Neil Brown CTD. Satellite images of sea surface temperature were obtained for the region during the period of sampling to determine the location of major oceanographic features.

Surface and oblique tows were taken at each station with bongo nets (70 cm diameter, 500 μm mesh). Oblique tows were taken to a maximum depth of 200 m or to within 10 m of the bottom. Depth and tow profiles were monitored in real time either by a submersible data logger attached to the frame of the bongo net (see Davis *et al.* (1990) for details) or by a SCANMAR depth-sensing unit. Surface nets were towed for 15 min from the side of the vessel. Volume filtered was calculated for each net by using calibrated General Oceanics flow meters. Numbers of larvae are standardized to 1000 m^3 volume filtered. For each tow, a sample from one side of the bongo was fixed in 4% formaldehyde (for identification) and the other in 95% ethanol (the latter for ageing). Larvae were identified from the descriptions by Bruce (1988, 1998).

Otolith analyses

The total ages (i.e. increment number + 6) of blue grenadier larvae were determined from otolith microstructure following the procedures of Thresher *et al.* (1988). Growth rates were calculated from body length (Leis and Trnski 1989) and are uncorrected for shrinkage. Statistical analyses used Statview FPU 4.02.

Increment widths were measured on the lapilli of 20 specimens via a computer-linked video system using the program Bony Parts (Brittnacher and Botsford 1994). Measurement protocols followed those of Thresher *et al.* (1988). Increment widths were compared between larvae collected from the eastern Victoria/southern NSW and Tasmanian waters. Ten larvae were selected from each area for analysis. Ages of larvae analysed ranged from 23 to 31 days (17–25 increments). Otoliths were read and processed 'blind' without knowledge of the location of capture. Comparisons of increment widths were made between the same increment number rather than increments formed on the same day (i.e. the width of the first increment was compared across all specimens irrespective of total age, then the second and so on). This was necessary to avoid the confounding effects of ontogenetic differences in increment widths (Bruce *et al.* in press).

Advection modelling

Circulation of the waters surrounding Tasmania and the south-east mainland was simulated by use of the three-dimensional non-linear hydrodynamic model referred to as MECO (Model of Estuaries and Coastal Oceans). This model has previously been applied to a range of estuarine and shelf systems, the most thoroughly documented being Port Philip Bay in Victoria (Walker 1996, 1999). It has also been used specifically for larval advection studies in the Gulf of Carpentaria (Condie *et al.* 1998).

Numerical solutions were computed on a latitude–longitude grid, which had been rotated through a false pole to cover a region from Albany in the west, across the Great Australian Bight and Tasmania, to a few hundred kilometres east of the Victorian coastline. There were 136 × 47 grid cells in the horizontal and 37 in the vertical. The horizontal resolution was ~20 km, and the vertical resolution expanded from 3 m near the surface to 200 m at the maximum model depth of 2000 m (interfaces at depths of 0, 3, 6, 9, 12, 15, 18, 22, 27, 33, 40, 48,

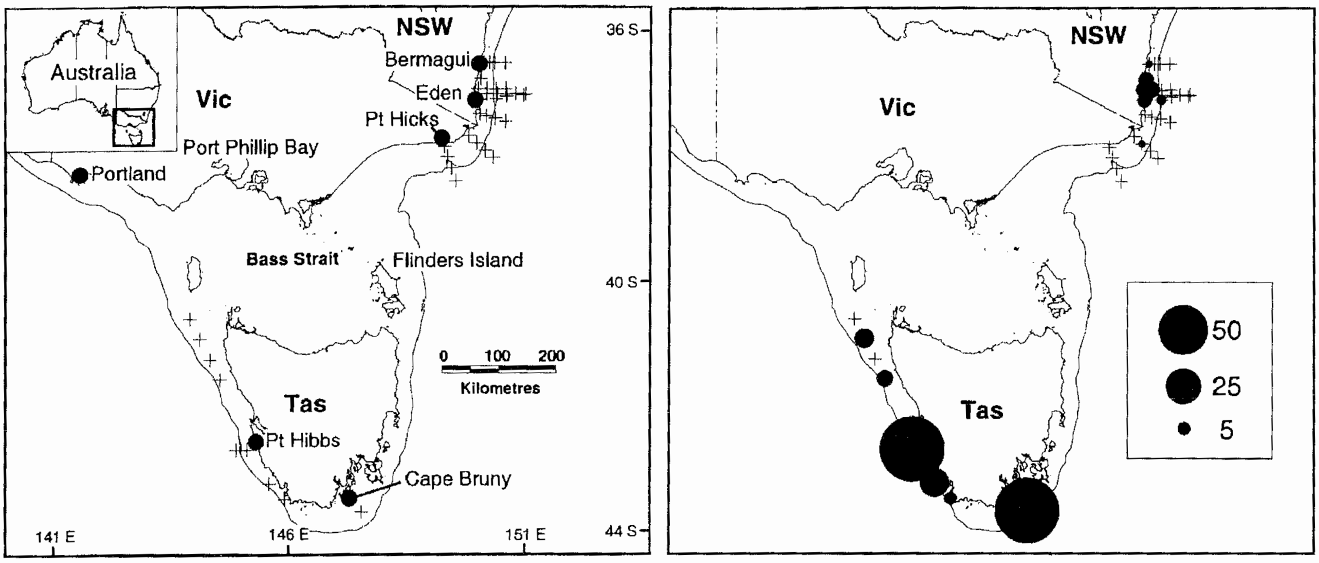


Fig. 1. Sampling sites and distribution of blue grenadier larvae in south-eastern Australia, August 1993. Larval abundance is expressed in numbers per 1000 m^3.

57, 67, 78, 90, 102, 116, 132, 150, 170, 195, 225, 260, 300, 350, 400, 500, 600, 700, 800, 900, 1000, 1200, 1400, 1600, 1800 and 2000 m).

Since the larvae tend to be found in regions of significant mean flow and are advected for periods much longer than a tidal cycle, high-frequency tidal motions were neglected. Model forcing was provided by seasonal climatologies of wind, sea level, temperature and salinity, with the focus on sub-inertial motions. The use of climatologies, rather than data from a specific time period, provides the subsurface temperature and salinity fields needed for open boundary forcing and interior data assimilation. The output of such a model provides 'typical' seasonal flow patterns, while effectively removing any influences associated with interannual variability.

Climatological winds were computed by vector-averaging winds from the National Center for Environmental Prediction (NCEP) reanalysis data set (Kalnay *et al.* 1996) over the 12 years from 1976 to 1997. This process gave 12 months of six-hourly climatological fields with a spatial resolution of ~200 km. Sea level, temperature and salinity fields were taken directly from the Climatology of Australian Regional Seas (CARS) seasonal climatology, which resolves the annual and semiannual harmonics on a 0.5° geographical grid (CSIRO Marine Research unpublished). The flow was forced by climatological winds over the surface, while sea level, temperature and salinity were specified at the open boundaries. Within the interior, sea level, temperature and salinity climatologies were assimilated through relaxation of the model values toward the climatological values. The relaxation time was set at 20 days for each field. The climatological fields were also used to initialize the model, which was first run for 20 days to allow transient effects associated with the initialization to dissipate. Blue grenadier larvae were represented in the model by neutrally buoyant particles, which were advected by the flow while also being dispersed through a random walk process. The entire model domain to a depth of 300 m was randomly seeded with 500000 particles. Each particle was tracked individually, so that particle movements could be traced back in time. This allowed spawning sites to be estimated from the observed location of capture and age of the larvae. No attempt was made to model the period between spawning at depth and eggs/larvae first reaching the surface mixed layer, which we estimate may take 1–2 days.

Results

Larval distribution

Blue grenadier larvae were most commonly collected off the west and south coast of Tasmania between Pt Hibbs and Cape Bruny (Fig. 1), where sampling at similar times of the year had previously recorded large numbers of larvae (Gunn *et al.* 1989).

Small numbers of larvae were also collected off southern NSW and eastern Victoria (referred to below as the mainland). Larvae recorded within this area were found at either inshore or mid-shelf stations, the single exception being a larva collected at the shelf edge off Eden. Blue grenadier larvae were largely confined to a cool water region bounded by a marked frontal feature on the shelf. The structure of plumes associated with this frontal feature (identified from satellite images of sea surface temperature, Fig. 2) suggested that this cooler water was part of an inshore northerly flow extending from eastern Bass Strait to just north of the Bermagui transect. Seaward of the frontal zone was a southerly flowing warm-water mass of East Australian Current origin extending as far south as central Tasmania.

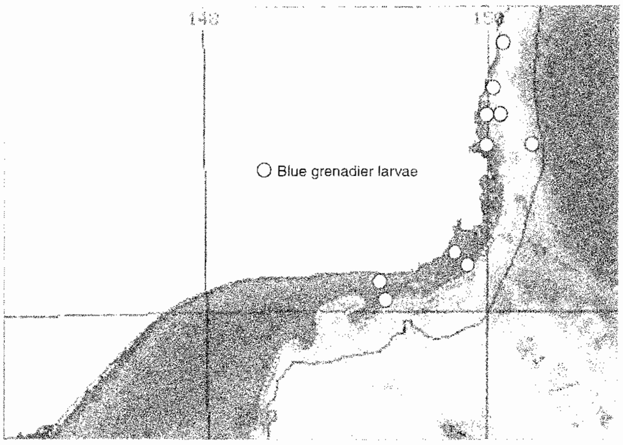


Fig. 2. Satellite image of sea surface temperature, August 1993. White dotted line denotes approximate position of frontal boundary between cool inshore northward-flowing water mass and warm water derived from the East Australian Current.

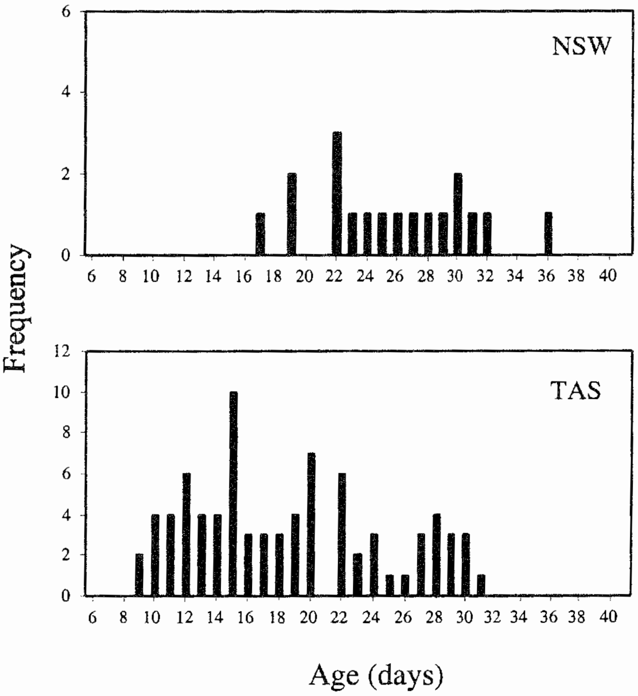


Fig. 3. Age distribution of blue grenadier larvae by area.

Ageing

Otolith microstructure was similar to that described for blue grenadier larvae by Thresher *et al.* (1988). Blue grenadier larvae collected from the western and southern Tasmanian coasts ranged from 3.1 to 8.6 mm body length and 9 to 31 days (total age). Larvae from the mainland were, on average, both larger and older than those from Tasmanian waters (5.3–14.5 mm and 17–36 days respectively, Fig. 3).

Age and size structure of larvae on the west and south coast of Tasmania were consistent with the well documented southward advection of larvae around Tasmania as described by Thresher *et al.* (1988) and Lyne and Thresher (1995). A pattern of age distribution in larvae from the mainland was less clear, although there was a tendency for larvae to increase in age northwards along the coast.

Back-calculated spawning dates varied between regions, with a trend for mainland larvae to have been spawned earlier than those from Tasmania (Fig. 4). For Tasmanian larvae, spawning was recorded essentially continuously (21 days over a 22 day period) from 24 July to 15 August, with no defined peak in spawning activity. Back-calculated spawning dates from mainland larvae were recorded on 14 days over a 22 day period between 13 July and 4 August.

Widths of the first 7–9 increments were similar in larvae from both areas, but rapidly diverged thereafter (Fig. 5). Subsequent increment widths were significantly larger in larvae from the mainland (paired *t*-test: $t = 8.749$, $P < 0.0001$). Larvae from both areas had the same pattern of increasing increment widths up until approximately increment 16, with widths then oscillated around means of ~3.6 µm (mainland) and 2.8 µm (Tasmania) respectively.

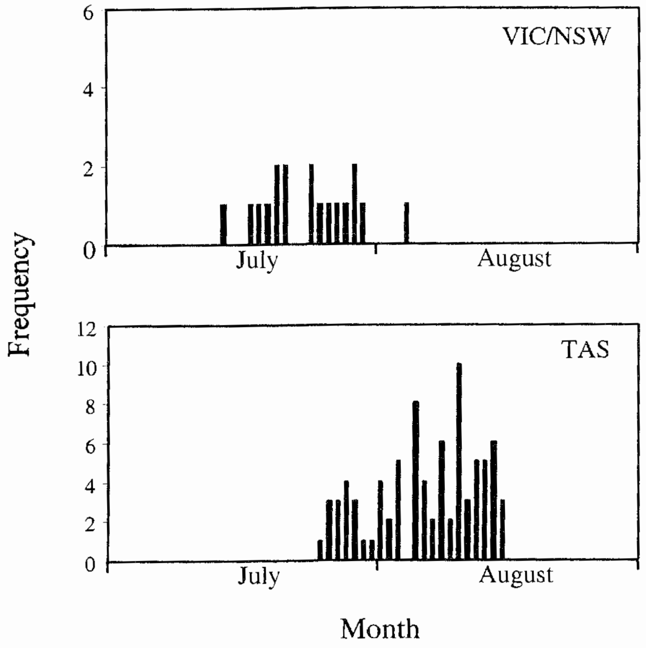


Fig. 4. Back-calculated spawning dates of blue grenadier larvae by area.

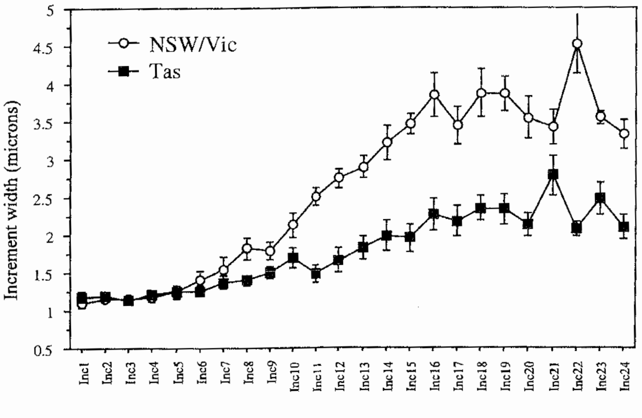


Fig. 5. Increment widths of blue grenadier larvae by area. Bar, 1 s.d.

Advection modelling

Model flows during the blue grenadier spawning period reveal strong coastal currents extending along the western flank of Bass Strait and around southern and eastern Tasmania (Fig. 6). This flow, known as the Zeehan Current (Baines *et al.* 1983), is a persistent feature on the west coast, but its effects are more seasonal in the east as a result of the encroachment of the East Australian Current during summer. The model currents off the west coast are consistent with long-term current-meter-mooring data with average current speeds of 0.3 m s^{-1} (Lyne and Thresher 1995). The recirculating patterns further offshore to the west are also evident in satellite drifter tracks (Cresswell, in press). After the model current passes around the south coast, it separates from the north-east coast of Tasmania and moves eastward towards New Zealand (Fig. 6). Ocean drifter tracks confirm this separation, although it tends to occur on the central east coast, with current speeds rarely exceeding 0.3 m s^{-1} (Cresswell, in press).

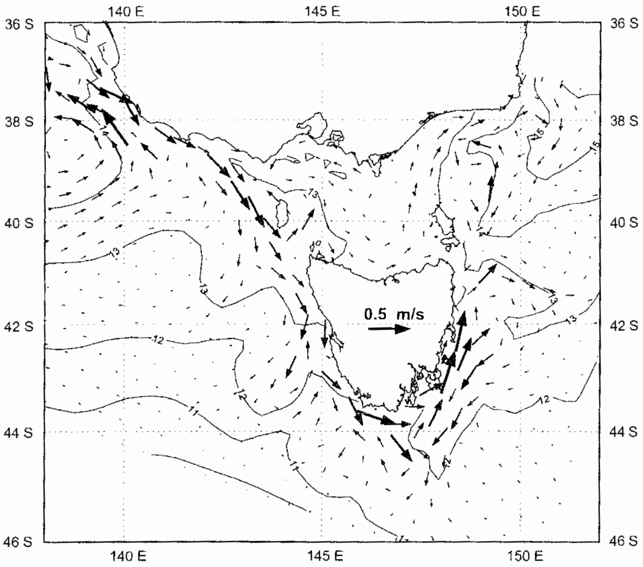


Fig. 6. Model current vectors and temperature contours (°C) at a depth of 20 m on 20 July.

The model currents within Bass Strait and along the south-eastern mainland shelf are generally much weaker than the Zeehan Current flows. Most of the eastward transport is initially concentrated in the southern half of the strait, before crossing to the north and exiting along the south-east mainland shelf. This current distribution is very similar to that obtained by Middleton and Black (1994) using a depth-averaged model with realistic wind and sea-level forcing and is consistent with satellite images of sea surface temperatures for this time of year. The flow in offshore waters immediately east of Bass Strait is dominated by an anticlockwise circulation in the model. Further offshore there is weak southward flow associated with the East Australian Current, whose core is much further to the north at this time of the year. These model outputs are also consistent with circulation features observed at this time of year.

The potential for larvae from the known spawning grounds off western Tasmania to reach the south-east region was first tested by tracking particles that were over these grounds at the mean spawning date (20 July). Particles starting within the top 100 m of this region were tracked for a month and their dispersion is shown at 10-day intervals (Fig. 7). A one-month period was selected because it covered the ages of most larvae collected from the south-east region and thus the time period required for transport to that area. Particles from the northern end of the spawning ground moved up to 100 km offshore to the south-west, before most returned to the west-coast shelf waters. However, the majority of particles followed the strong coastal current around southern Tasmania, then tracked north along the east coast before turning offshore into the Tasman Sea. There was no evidence of particles from the Tasmanian west coast approaching the mainland region where blue grenadier larvae were caught.

A more systematic approach to identifying potential spawning grounds is to identify particles approximately coincident in time and location with the capture of each larva and track them back in time to the spawning date estimated from the otolith analysis. The closest 20 particles to each blue grenadier larva caught in mainland waters were identified and tracked back in time to the back-calculated spawning date. The region defined by this cluster of particles at the spawning date then provided an estimate of the potential spawning location. The particle clusters derived from all the mainland larval catches are shown in Fig. 8. The potential spawning region forms a tight band along the south-eastern Victorian shelf, then spreads south across eastern Bass Strait. The complex flow patterns east of Bass Strait also entrain a smaller number of particles from further offshore over the continental slope and deep ocean.

The points in Fig. 8 are not necessarily representative of actual spawning sites. Blue grenadier are known to spawn over the upper slope in 400–600 m of water. This is followed by a short period (estimated by us to be ~1–2 days) in which the eggs and young larvae rise up into the surface mixed layer (presumably as a result of their positive

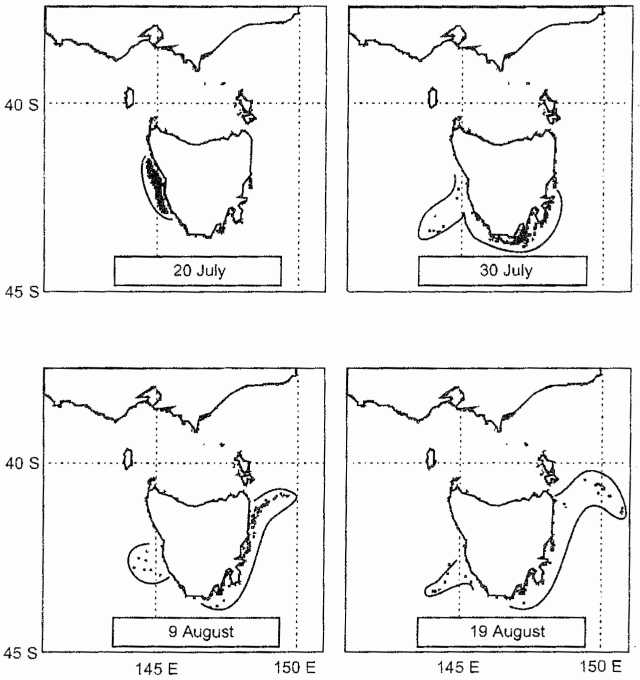


Fig. 7. Modelled dispersion of particles seeded off the west coast of Tasmania on 20 July. Lines denote the range of particle clouds, and their distribution is shown 10, 20 and 30 days after seeding.

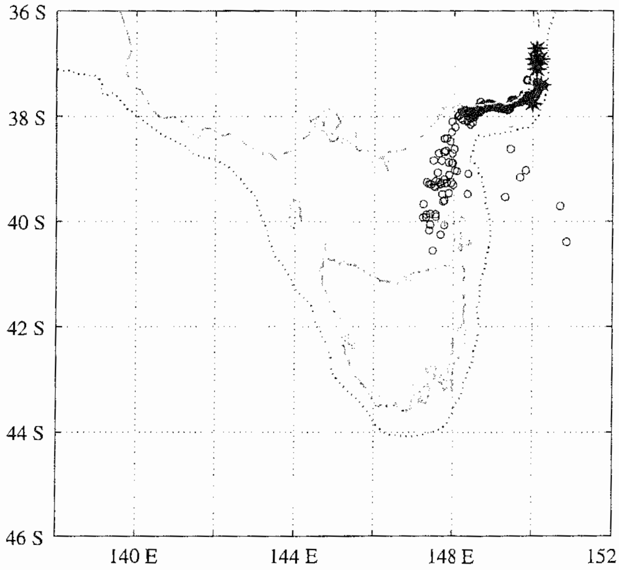


Fig. 8. Locations of particles approximately coincident in space and time with the capture of blue grenadier larvae, after tracking back in time to the spawning date (○). Capture locations of larvae used in the analyses (*) and 500 m depth contour (dotted line) are also shown.

buoyancy), where they usually first appear over the shelf. This initial vertical migration is not represented in the model. However, the horizontal advection during this period is expected to be small and primarily from the upper slope onto the shelf. Figure 8 therefore suggests that larvae caught off the mainland are consistent with either spawning on the nearby slope or spawning further south on the slopes of eastern Bass Strait.

Discussion

Our discovery of blue grenadier larvae off southern NSW and eastern Victoria supports the hypothesis of Thresher *et al.* (1988) that the species may have more than one spawning ground in southern Australia. Their study reported finding small numbers of blue grenadier larvae east of Flinders Island, but they failed to record any off southern NSW or eastern Victoria; their survey in these latter areas was restricted to the shelf edge which, on the basis of our observations, would fail to sample the cooler inshore water where we found larvae. Satellite records (1988–94) indicate that this cooler inshore water mass is a consistent feature of the inner shelf region during June–August.

Comparison of back-calculated spawning dates for larvae from both Tasmania and the mainland indicate a trend towards earlier spawning in the latter. A pattern of earlier spawning in larvae from the mainland than from Tasmanian waters has been reported for several other species (Bruce *et al.* in press and 2001). However, both ranges of spawning date fall well within the spawning period previously documented for blue grenadier on western Tasmanian grounds (Gunn *et al.* 1989). Thus, if the mainland larvae originated from a second spawning ground, it is likely that this spawning is roughly simultaneous with western Tasmania. Simultaneous spawning at different spawning grounds is also a feature of blue grenadier populations in New Zealand (Livingston 1990).

There are three potential scenarios regarding the source of the mainland blue grenadier larvae. First, larvae may have originated from the area where they were caught. Second, larvae may have originated from the well documented western Tasmanian spawning grounds and may have been advected from there to the sampling area. Third, larvae may have originated from a second, as yet unidentified, spawning area separate to either of the above.

The absence of either eggs or small larvae <10 days of age, the location of larvae within an inshore northward-flowing water mass, and the pattern of increasing age with distance north along the coast, all suggest that the mainland larvae were not from local spawning but from a more southerly source. The only larva captured outside the cool inshore water (from near the shelf break off Eden) was the largest and oldest (14.5 mm, 36 days) collected and most likely had become entrained in the southward-flowing East Australian Current after originally being part of the northward flow.

The similarity of increment widths between specimens from Tasmania and the mainland for the first 6–10 days after first feeding suggests that *(i)* larvae originated from the same locality and subsequently moved into separate water masses, *(ii)* larvae were spawned in different areas but experienced similar initial growth conditions or *(iii)* that increment widths are initially ontogenetically determined and poorly reflect growth characteristics for the first 6–10 days after first feeding. The present data cannot distinguish between these possibilities. However, increment widths in other species have been shown to correlate well with somatic growth (Mugiya and Oka 1991, Fowler and Short 1996) and have been used to identify larvae of different sources within south-eastern Australia (Bruce *et al.* in press).

The normal advection pathway for blue grenadier larvae from western Tasmania spawning grounds is southwards to nursery areas on the south and east coasts of Tasmania (Thresher *et al.* 1988). The mean rate of advection previously observed (0.1–0.2 m s^{-1}) falls within the range of our advection model (0.1–0.5 m s^{-1}) and is consistent with previous empirical and modelled longshore currents (Lyne and Thresher 1995). This implies a largely passive transport mechanism. Indeed, our observations, based on ages of larvae collected during sampling of the west and south coasts of Tasmania, support such southerly transport. However, the advection rate required to transport larvae via this southerly route around Tasmania and then north to southern NSW (a distance of 1050–1250 km) in 17–36 days is 0.5–0.7 m s^{-1}. This is well in excess of that previously recorded and is not reflected in the model particle advection rates (Fig. 7). This suggests that if the mainland larvae had originated from western Tasmania they could not have been transported via the normal southern Tasmanian route.

The shortest distance between western Tasmania and southern NSW is through Bass Strait. Recent ichthyoplankton sampling in Bass Strait, however, failed to find any blue grenadier larvae (F. J. Neira, Australian Maritime College, personal communication). Given the age of blue grenadier larvae collected from the mainland and the distance from the western Tasmanian spawning grounds (650–850 km), a mean advection rate of 0.3–0.4 m s^{-1} would be required to transport larvae to the south-east region. Thresher *et al.* (1988) did note that a small number of drift cards released over west-coast spawning grounds tracked north and were returned from King Island, western Victoria and Western Port Bay. One card was also returned from south-east mainland Australia, although this was after several months and it was unclear whether it had followed a path around southern Tasmania or through Bass Strait.

Winds are a major influence on the circulation in Bass Strait, and during the month leading up to the larval sampling these were very similar to the climatological fields used to force the advection model (5–8 m s^{-1} from west-north-west). The circulation within Bass Strait generated by the model at this time of year consisted of a meandering current stretching from north-west Tasmania across to the mainland where the sampling occurred (Fig. 6). Very similar flow patterns have also been obtained with a depth-averaged model with real-time wind data and sea-level forcing (Middleton and Black 1994). However, in both models the current speeds are well below those required to carry larvae from western Tasmania to the mainland within the age period of the larvae. When particles were tracked in our model from north-western Tasmania, they were carried north-eastwards into Bass Strait, but after 30 days had only moved approximately half way across the strait.

There are unconfirmed observations, by commercial fishers, of ripe blue grenadier from two areas outside the west Tasmanian spawning ground — south of Portland (western Vic.) and eastern Bass Strait. These areas provide possible sources for the mainland larvae. Calculations similar to those above suggest that advection rates of 0.3–0.4 m s^{-1} would be required to transport larvae the 750–950 km from Portland to our sampling area, again well exceeding observed and modelled rates.

Advection rates required to transport larvae from eastern Bass Strait are far more realistic. The advection modelling, combined with the observed continuity of water properties (from SST), suggests that the mainland larvae were likely to originate somewhere along the slope between the sampling region and eastern Bass Strait/Flinders Island. The latter is the same region where Thresher *et al.* (1988) reported small numbers of blue grenadier larvae; hence, our data further support their conclusions regarding spawning in the area. Neither the annual regularity nor the exact location of this spawning event can yet be determined. Juvenile blue grenadier (<30 cm) have been recorded in some years from outer shelf and slope waters of southern NSW and eastern Victoria (J. Garvey, Bureau of Resource Sciences, Canberra, personal communication) suggesting either irregular spawning in, or irregular recruitment to, the area.

In summary, our data further support the presence of a second spawning area for blue grenadier in south-eastern Australia. On the basis of the age of larvae and modelled advection patterns, this spawning area is most probably off eastern Bass Strait as originally hypothesized by Thresher *et al.* (1988). The exact location, annual regularity and magnitude of this spawning event are not yet known, nor whether spawning in this area represents a separate stock or represents a satellite spawning ground for adults that do not always migrate to the western Tasmanian grounds. That no significant aggregations of blue grenadier have been reported from eastern Bass Strait by commercial fishers suggests that spawning in the area is on a minor scale relative to the western Tasmanian grounds.

Acknowledgments

The authors thank C. Bulman and A. Koslow for their constructive comments on earlier versions of the manuscript and J. Mansbridge for programming support. MECO was developed at CSIRO Marine Research by Stephen Walker and Jason Waring. This work was supported by grants 92/019 and 98/103 from the Fisheries Research and Development Corporation.

References

Annala, J. H. (1995). Report from the Fishery Assessment Plenary, May 1995: stock assessments and yield estimates. (MAF Fisheries: Wellington. NZ.) 277 pp.

Baines, P. G., Edwards, R. J. and Fandry, C. B. (1983). Observations of a new baroclinic current along the western continental slope of Bass Strait. *Australian Journal Marine and Freshwater Research* **34**, 155–7.

Brittnacher, J., and Botsford, L. (1994). Bony parts: an image analysis program. (University of California: Davis, CA.)

Bruce, B. D. (1988). Larval development of blue grenadier, *Macruronus novaezelandiae* (Hector), from Australian waters. *Fishery Bulletin(US)* **86**, 119–28.

Bruce, B. D. (1998). Macruronidae — hakes. In 'The Larvae of Temperate Australian Fishes, a Laboratory Guide for Larval Fish Identification'. (Eds F. J. Neira, A. G. Miskiewicz and T. Trnski.). pp. 88–91. (University of Western Australia Press: Nedlands, Australia.)

Bruce, B. D., Sutton, C. A. and Thresher, R. E. (1996). An ichthyoplankton based analysis of the spawning distribution and stock structure of temperate Australian fin-fish. Final report to Fisheries Research and Development Corporation. CSIRO Hobart, Australia. 65 pp.

Bruce, B. D., Young, J. W., Evans, K., Sutton, C. A., and Furlani, D. M. (in press). The influence of mesoscale oceanographic processes on larval distribution and stock structure in jackass morwong (Teleostei : Cheilodactylidae). *ICES Journal of Marine Science*

Bruce, B. D., Neira, F. J., and Bradford, R. W. (2001). Larval distribution and abundance of blue and spotted warehous (*Seriolella brama* and *S. punctata*: Centrolophidae) in south-eastern Australia. *Marine and Freshwater Research* **52**, 631–6.

Condie, S. A., Loneragan, N. R., and Die, D. J. (1999). Modelling the recruitment of tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) to nursery grounds in the Gulf of Carpentaria, northern Australia: implications for assessing stock-recruitment relationships. *Marine Ecological Progress Series* **178**, 55–68.

Cresswell, G. (in press). Currents of the continental shelf and upper slope of Tasmania. *Proceedings of the Royal Society of Tasmania*

Davis, T. L. O., Jenkins, G. P., and Young, J. W. (1990). Patterns of horizontal distribution of the larvae of southern bluefin (*Thunnus maccoyii*) and other tuna in the Indian Ocean. *Journal of Plankton Research* **12**, 1295–314.

Fowler, A. J., and Short, D. A. (1996). Temporal variation in the early life-history characteristics of the King George whiting (*Sillaginodes punctata*) from analysis of otolith microstructure. *Marine and Freshwater Research* **47**, 809–18.

Gunn, J. S., Bruce, B. D., Furlani, D. M., Thresher, R. E., and Blaber, S. J. M. (1989). Timing and location os spawning of blue grenadier, *Macruronus novaezelandiae* (Teleostei : Merlucciidae) in Australian coastal waters. *Australian Journal of Marine and Freshwater Research* **40**, 97–112.

Kailola, P. J., Williams, M. J., Stewart, P. C., Reichelt, R. E., McNee, A., and Grieve, C. (1993). 'Australian Fisheries Resources.' (Bureau of Rural Resources and Fisheries Research and Development Corporation: Canberra.)

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., *et al.* (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society* **77**, 437–71.

Leis, J. M., and Trnski, T. (1989). 'The Larvae of Indo–Pacific Shorefishes.' (University of New South Wales Press, Sydney.)

Livingston, M. E. (1990). Spawning hoki (*Macruronus novaezelandiae* Hector) concentrations in Cook Strait and off the South Island, New Zealand, August–September 1987. *New Zealand Journal of Marine and Freshwater Research.* **24**, 503–17.

Livingston, M. E., and Schofield, K. A. (1996). Stock discrimination of hoki (*Macruronus novaezelandiae*) in New Zealand waters using morphormetrics. *New Zealand Journal of Marine and Freshwater Research* **30**, 197–208.

Lyne, V. D., and Thresher, R. E. (1995). Dispersal and advection of *Macruronus novaezelandiae* larvae off Tasmania: simulation of the effects of physical forcing on larval distribution. In 'Multidisciplinary studies of Recruitment of Australian Marine Populations'. (Ed. P. Sammarco.) (American Geophysical Union: Washington, DC.)

Middleton, J. F., and Black, K. P. (1994). The low frequency circulation in and around Bass Strait: a numerical study. *Continental Shelf Research* **14**, 1495–521.

Milton, D. A., and Shacklee, J. B. (1987). Biochemical genetics and population structure of blue grenadier, *Macruronus novaezelandiae* (Hector) (Pisces : Merlucciidae), from Australian waters. *Australian Journal of Marine and Freshwater Research* **38**, 727–42.

Mugiya,Y., and Oka, H. (1991). Biochemical relationship between otolith and somatic growth in the rainbow trout *Oncorhynchus mykiss*: consequence of starvation, resumed feeding, and diel variations. *Fishery Bulletin* **89**, 239–45.

Murdoch, R. C. (1992). A review of the ecology of hoki, *Macruronus novaezelandiae* (Hector), larvae in New Zealand waters. In 'Larval Biology'. (Ed. D. A. Hancock.) Australian Society for Fish Biology Workshop, Hobart, 20 August 1991, Bureau of Rural Resources Proceedings No. 15. (AGPS: Canberra.)

Murdoch, R. C., and Chapman, B. E. (1989). Occurrence of hoki (*Macruronus novaezelandiae*) eggs and larvae in eastern Cook Strait. *New Zealand Journal of Marine and Freshwater Research.* **23**, 61–7.

Thresher, R. E., Bruce, B. D., Furlani, D. M., and Gunn, J. S. (1988). Distribution, advection and growth of larvae of the southern temperate gadoid, *Macruronus novaezelandiae* (Teleostei : Merlucciidae), in Australian coastal waters. *Fishery Bulletin (US)* **87**, 29–48.

Walker, S. J. (1996). Hydrodynamic models of Port Phillip Bay. Technical Report No. 38, CSIRO Port Phillip Bay Environmental Study, Melbourne, Australia.

Walker, S. J. (1999). Coupled hydrodynamic and transport models of Port Phillip Bay, a semi-enclosed bay in south-eastern Australia. *Marine and Freshwater Research* **50**, 469–81.

Zeldis, J. R., Murdoch, R. C., Cordue, P. L., and Page, M. J. (1998). Distribution of hoki (*Macruronus novaezelandiae*) eggs, larvae and adults off Westland, New Zealand, and the design of an egg production survey to estimate hoki biomass. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1682–94.

Manuscript received 22 November 1999; revised and accepted 18 September 2000

Mar. Freshwater Res., 2001, **52**, 611–22

Spawning dynamics of the eastern gemfish (*Rexea solandri*) in relation to regional oceanography in south-eastern Australia

Jeremy D. Prince[A] *and David A. Griffin*[B]

[A]Biospherics Pty Ltd, PO Box 168, South Fremantle, WA 6162, Australia
[B]CSIRO Division of Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia

Abstract. Experienced fishers believe the winter aggregations of gemfish are influenced by the following: cold bottom currents from the south and east flowing up onto the shelf; the edge of warm-core eddies; and topographic features along the shelf break. These claims were tested through observations made at sea during industry surveys of the winter gemfish seasons 1996–98, and the study of 250 m isotherm charts, sea surface temperature data, and historic catch data. The study generally confirmed the anecdotal information collected from the fishers. The first gemfish aggregations of the winter season often form on the southern edge of a warm-core eddy. Secondarily, aggregations tend to form around the northern edge of the warm-core eddy if it is interacting with the shelf break. Finally, gemfish aggregate around the point at which the main flow of the East Australian Current (EAC) detaches from the continental shelf. This timing and location apparently coincides with conditions conducive to the production of subsurface plumes of nutrient-rich deep Sub-Antarctic mode Water. These plumes lead to seasonal enhancement of phytoplankton growth along the edge of the continental shelf, which may offer the adaptive advantage of enhancing the survival and growth of larval gemfish.

Introduction

Eastern gemfish (*Rexea solandri*) is an oceanic midwater species caught along the edge of the continental shelf of southern Australia and New Zealand by demersal trawling and droplining (Paulin 1997). During summer, sub-adult fish are caught scattered along the eastern Tasmanian shelf break and aggregated around canyons. However, during winter, dense targetable aggregations of mature adults move along the shelf break off southern New South Wales (NSW) and become vulnerable to demersal trawling in 360–440m.

The demersal trawl fishery for eastern gemfish began in the late 1960s when trawl fishermen operating out of Newcastle and Sydney first discovered the winter aggregations of gemfish between 33° and 34°S. The fishery developed rapidly as fishers to the south discovered that these aggregations began developing in early winter as far south as canyons of eastern Bass Strait, the Horseshoe and Smithy's Corner (38°S). Catches from the fishery peaked in 1978–80 with recorded landings of ~5000 t year^{-1} (Rowling 1990). The fishery remained unmanaged through most of the 1980s with annual catches of ~3000–4500 t.

Monitoring of the size composition of the catch detected a decline in recruitment during the late 1980s (Rowling 1990) leading to a 60–70% decline in spawning biomass by the late 1980s (Eastern Gemfish Assessment Group 2000). This led to the introduction of management measures to reduce catches. In 1988 a 3000 t total allowable catch (TAC) for trawl catches was introduced for eastern gemfish to control and reduce catches. The targeted catch was progressively reduced to zero by 1993, and with the exception of 1997 the fishery has remained closed to targeted fishing because of concern about low stock size resulting from an extended period of low recruitment.

The Eastern Gemfish Assessment Group has identified the strategic importance of developing fishery-independent indices of stock abundance for eastern gemfish, as used to monitor populations of many marine fish species. Fishery-independent surveys often concentrate on surveying spawning aggregations because a high percentage of the adult stock is assumed to be available for surveying at that stage. But design and implementation of surveys of breeding aggregations require an understanding of aggregation dynamics, specifically factors influencing the timing and location of spawning. In the case of the eastern gemfish this knowledge is lacking.

Since 1993 a series of industry-based surveys of the eastern gemfish winter season (Prince and Wright 1994; Prince 1996,1999; Prince *et al.* 1997, 1998*a*) has primarily aimed to provide indices of stock abundance (catch per unit effort) for the annual stock assessment by the Eastern Gemfish Assessment Group and size composition data. A subsidiary aim of the surveys has been to study the aggregation dynamics of eastern gemfish, in particular

10.1071/MF00007 1323-1650/01/040611

factors that influence timing and location. This paper documents this aspect of these studies.

Methods

During the initial industry survey of 1993, G. Wright began formally interviewing experienced gemfish fishers (Prince and Wright 1994), and in succeeding years this body of fisher lore has been consolidated by the use of a 'snowball' approach to interviewing fishers (Neis *et al.* 1999) rather than a random sampling process. Random sampling procedures may document general information, but only a more directed sampling process can collect specialized and commercially sensitive knowledge held by only a few experts unevenly distributed through a fishing community. Local 'experts' have been consulted formally and informally. As has been noted (Neis *et al.* 1999) the observations of the best fishers are almost invariably correct, even when their interpretation may be faulted.

This body of fisher lore has led to hypotheses to be tested with data drawn from the following sources: the literature on the region's oceanography and personal communications from oceanographers in CSIRO; sea surface temperature satellite imagery and reports of commercial catches in the South East Fishery (SEF1); isotherm charts for 250 m compiled for the region by Royal Australian Navy METOC Service; and our field experience through the industry surveys of 1996–99 and temperature–depth profiles we collected through the surveys.

Fisher lore

Rowling *et al.* (1990) have documented the northward along-shelf progression of a winter eastern gemfish season, through June and August 1989.

In gemfish, as with most other SEF species, catchability is related to the aggregation behaviour of the species. During most of the year gemfish are not aggregated near the trawl grounds and are not caught by trawling. In some summers, dispersions of juvenile and sub-adult gemfish occur over the southern upper-slope trawl grounds and small catches become possible. Gemfish fishers recognize the onset of the winter season because in the preceding month sub-adult gemfish become catchable in small quantities over a wide range of depths (200–600 m). Through the entire winter season and sometimes for 1–2 months afterwards sub-adult fish remain slightly catchable over a wide depth range (Prince *et al.* 1998*a*).

The depth range within which gemfish spend most time is unknown. Scientists and managers tend to view most SEF species as predominantly demersal because they are caught with demersal trawls along narrow, relatively precisely depth-delineated strips of the continental slope (Prince *et al.* 1998*b*). But the fishers believe gemfish to be pelagic and to forage over a wide depth range and away from the slope through the oceanic midwaters. Paulin (1997) notes their association in New Zealand waters with their mesopelagic prey, lanternfish (Myctophidae). Off NSW in winter, a cursory examination of gemfish stomachs (Prince, unpublished) revealed that many of them are feeding, those with food in their stomach generally having a single item of prey in varying stages of digestion; the prey found has been almost exclusively jack mackerel (*Trachurus declivis*) and southern frostfish (*Lepidopus caudatus*), two mesopelagic piscivores (Blaber and Bulman 1987).

Initially during the winter the catchability of mature gemfish increases only slightly in the core gemfish depths (360–440 m) as a scatter of gemfish moves over the trawl grounds. Along the 'gemfish line' (360-440 m) a low catch of mature gemfish (5–25 kg h^{-1}) can almost always be taken during the main winter season. The gemfish season itself comprises a dramatic increase in the catchability of mature gemfish that occurs during the spawning migration of the gemfish. Fishers say that in the days preceding the gemfish season sea surface temperatures fall rapidly by 2–5°C.

When fishing for gemfish, fishers searched for aggregations along the gemfish line, using their sounders and conducting exploratory trawls.

The fishers say that only on rare occasions can gemfish aggregations be detected with their echosounders (Prince *et al.* 1998*a*). However, during the gemfish season they expect gemfish to be within the deep scattering layer, which they call the 'feed layer' because it is known to contain the prey species of gemfish and other commercial species. Therefore, with their sounders the fishers search for heavy feed layers preferably at the bottom in ~400 m. The fishers believe that the species within the deep scattering layer are vulnerable to their demersal nets only when within 2–4 m of the bottom, i.e. below the height of their headlines.

Because of the low acoustic detectability of gemfish, targeted gemfish fishing basically involves searching for areas of thick deep scattering layer and then conducting trial trawl shots to sample species composition. The first trawl shot of the day is normally timed to begin around dawn when the 'feed layer' dives towards the bottom. However, the fishers say that midday can also be a good time to catch gemfish because the sunlight is strongest at that time and gemfish will be close to the bottom avoiding the daylight. At other times the highest catch rates can be observed in afternoon trawl shots (Prince 1996).

When fishing or searching for gemfish the fishers generally tow their demersal trawl nets from north to south because catch rates have been proved to be highest in this direction. They believe that the fish are swimming northward along the shelf break, and that at slow towing speeds (<2 knots) the gemfish can be herded into the throat of the net and towards the cod-end before being alarmed by the presence of the net. One fisher likened gemfish trawling to the use of traditional fixed-position freshwater-eel traps.

To this end, purpose-built gemfish nets had large and long throats of relatively light netting to reduce pressure waves and entrap gemfish.

Targeted gemfish trawls tend to be long (3–6 h) and are not targeted at any specific acoustic mark or feature. Instead, a well established soft-bottomed trawl ground is worked parallel to the contours of the continental slope, thereby maximizing trawling time in 360–440 m (Prince *et al.* 1997). Some of the best gemfish trawl grounds are adjacent to abrupt topographic features such as canyons or bluffs. The same trawl grounds are trawled repeatedly during a gemfish season and it is not unusual for exactly the same trawl ground to be trawled multiple times within a single day.

Certain points along the shelf edge, where there are canyons and bluffs, appear to preferentially attract aggregations of gemfish. Occasionally, the formation and dispersion of an aggregation will be observed in one of these areas by fishers repeatedly trawling in the same locality (Prince *et al.* 1998*a*). In these situations, catch rates may vary among shots from 10s to 1000s of kilograms per hour as the same trawl ground is trawled over several days. Thus, compared with the stability of orange roughy aggregations (Pankhurst 1988; Elliott and Kloser 1993; Koslow *et al.* 1995), on hourly and daily time scales, gemfish aggregations are ephemeral and mobile.

Although the aggregations generally proceed from south to north along the shelf during each winter season, the aggregations do not necessarily move continually north. Not all the historically favoured points will attract gemfish aggregations in each year. Instead, aggregations may apparently skip among favoured 'edge of canyon' grounds.

In 1993, Wright found that gemfish fishers regarded the movement and behaviour of the gemfish aggregations within each winter season to be relatively variable (Prince and Wright 1994). His recorded interviews showed that they attributed much of the variability of the gemfish season to regional oceanography and its interaction with topographical features along the shelf break.

This is illustrated here by comments from two experienced Ulladulla fishermen recorded by Wright:

'See, on the shelf the winter months are the best because the tide is slack and you get dirty water and the feed, so fish come around. During the summer we get hot water currents running down from north to south. The water turns really blue. There's nothing in it. The feed goes away or the current takes the food away. There's nothing, it is dead water. That's why during summer time we don't go to the shelf, because we catch nothing. ... Down there at Eden in the South they've got better catch rates than here on the east coast. And I believe that's because they are less affected by the warm current on the east coast.'

The next comments were made as a fisher sketched an illustration onto a piece of paper. Figure 1 is drawn from Prince and Wright (1994) and reproduces the fisher's sketches.

'These big eddies, big currents, scream out to sea, really hard, in these places. It creates a fence, a barrier. And the gemfish travelling north get as far as the top of this canyon and stops. It stops there for two weeks ... And the Ulladulla boats have had big seasons. As soon as the current shifts – the fish go through like a rocket.

Now the same situation applies down here ... at Gabo Island. You have trawl grounds [on either side of a substantial canyon] and you have the same effect. It seems to be [that the eddying is a consequence of] these headlands jutting out has some impact on the currents. It sometimes creates a barrier for the fish at the Gabo Ground. But not as strong as on the Ulladulla ground.'

During the interviews the fishers of NSW described how warm clear water with a distinctive deep blue colour flows from the north for most of the year. It flows from the north most strongly during summer and is clear and blue because

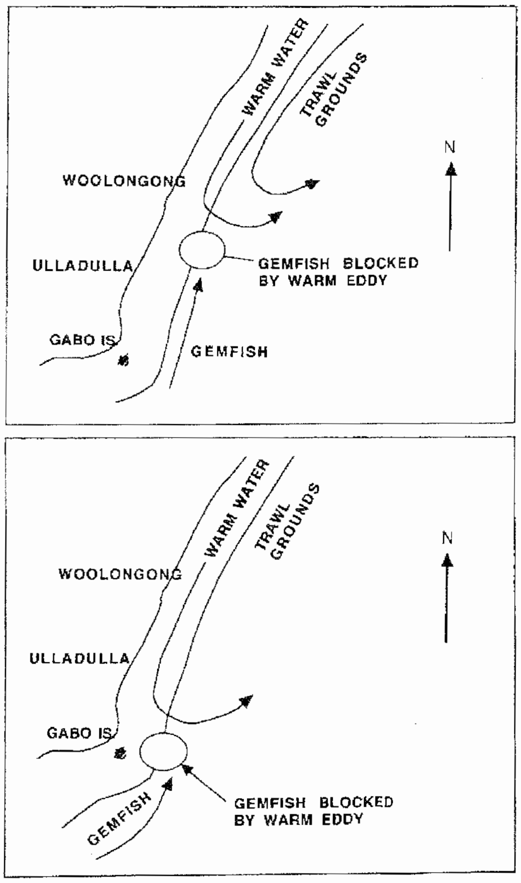


Fig. 1. Factors affecting the aggregation of eastern gemfish, as drawn by an experienced gemfish fisher from Ulladulla. (From Prince and Wright 1994.)

it has no plankton or 'feed'. Experienced gemfish fishers believe that the timing and location of spawning gemfish aggregations is linked to the movement of cold deep water that flows along and onto the shelf, against the warm clear summer water during winter. This winter water from the south and east brings green water that is 'dirty' with plankton.

They believe that the gemfish drift north along the shelf break with the deep cold 'tide' from the south and south-east, sporadically forming aggregations (Prince and Wright 1994; Prince *et al.* 1998*a*). According to the fishers, the gemfish sometimes 'bank up', and form aggregations that may remain stationary for several weeks, aggregating, dispersing and re-aggregating sporadically in the same area. They believe this occurs when the gemfish run into the warm currents flowing from the north, either around warm-core eddies interacting with the shelf edge, or at the edge of the main flow of EAC water.

Regional oceanography of the study area

Eastern gemfish inhabit the most productive of Australia's coastal seas, the Tasman, which can loosely be defined as the region between the Tasman front and subtropical front. For reviews of the physical oceanography of the Tasman Sea, see Church and Craig (1998) and Tomczak and Godfrey (1994).

The dominant external influences on the water masses of the upper Tasman Sea are the EAC to the north and the subtropical front to the south. The EAC is the western boundary current of the South Pacific and brings warm, saline water southwards along the East Australian margin. At some point off the New South Wales shelf, the main core of the current detaches and heads east along the turbulent Tasman Front towards the northern tip of New Zealand. The detachment process is far from steady. It has a slow, seasonal (north in winter) migration (Ridgway and Godfrey 1997) and also rapid transitions, sometimes associated with the pinching-off of loops to form warm core eddies (Nillson and Cresswell 1981) that eventually dissipate in the Tasman.

Although EAC waters do not penetrate to the depths at which gemfish are usually caught, the EAC and, particularly, its eddies have a strong indirect influence through large vertical displacements of the entire water column. Secondary circulation associated with these disturbances, although still only poorly understood, is known to often have a strong up- or down-slope component. Western boundary currents (and the eddies they shed) displace the cooler ocean waters in their path, establish sharp temperature fronts at the interface, and interact with waters of the continental shelf (Tranter *et al.* 1986). Fast currents along the coastal edge of warm-core eddies and EAC meanders carry surface filaments or streamers of warm water from the upstream source of the EAC and at the shelf break create counter currents that draw subsurface plumes of cooler water up the continental slope. The proximity of warm-core eddies and meanders to the shelf break, current strength and northerly winds determine the extent of slope intrusions (Tranter *et al.* 1986).

Intrusions of deep water along the southern NSW shelf support annual blooms of phytoplankton that contain some of the highest densities measured in Australian waters (Hallegraeff and Jeffrey 1993).

In contrast to the EAC, the direct influence of the subtropical front is at depths greater than those where gemfish are found. The subtropical front forms the southern (40°S in the Tasman) boundary of the Subtropical convergence, the region where mean winds drive downwelling through Ekman pumping. Deep winter mixing near the front produces Sub-Antarctic mode Water, which sinks and moves slowly northward, forming, off eastern Australia, a thick (hence 'mode') layer of water at ~9°C and 34.6 salinity at ~500 m. Much less is known about the variability and energetics of this deep, much less easily observed water mass, although it is safe to say that variability would be much less than near the surface. The annual cycle of temperature, for example, is negligible in comparison with that of the EAC.

To summarize, the 300–400 m depth stratum in which gemfish are found is sandwiched between the relatively quiescent, constant environment of the Sub-Antarctic mode Water and the dynamic EAC.

Observations of the winter gemfish seasons 1996–98

During the winter gemfish seasons of 1996–98 we placed scientific monitors aboard a range of commercial vessels central to stock assessment by the Eastern Gemfish Assessment Group. In 1997 there was a small commercial TAC and the observers monitored commercial fishing. During 1996 and 1998 no targeted commercial fishing of gemfish aggregations was allowed. Monitored vessels used research quota to sample gemfish aggregations. Close liaison on a daily basis with the entire commercial trawling fleet off southern NSW, the examination of catches landed by other vessels and SEF1 catch and effort reports provided the context for the documented activities of the monitored vessels.

Regional oceanographics during the seasons 1996–98 were studied on weekly 250 m isotherm charts produced for the study area by the Royal Australian Navy's METOC services. During 1997 and 1998, access to single-pass sea surface temperature (SST) imagery through the Remote Sensing Unit of CSIRO, Hobart, allowed SSTs to be monitored every 4 h in cloud-free areas.

1996

In the first episode (22–26 June), survey catches (Fig. 2*left*) were clustered to the south-east of Ulladulla (35.7°S) near the point at which the EAC detached from the shelf (Prince 1996). This point became the southern edge of a new warm-

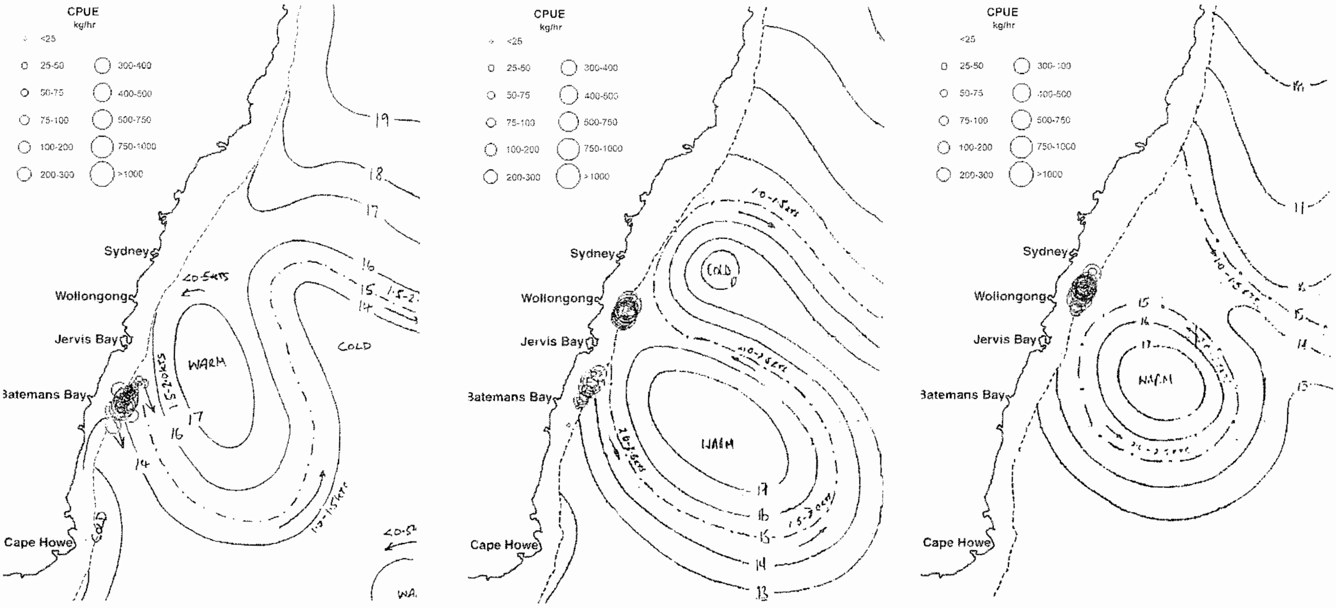


Fig. 2. METOC 250 m isotherm charts for winter 1996 overlaid with gemfish catch rates (kg h^{-1} by shot) observed during the 1996 industry survey (Prince 1996): *(left)* 26 June with catch data up to 30 June, *(centre)* 17 July with catch data 1–20 July and *(right)* 31 July with catch data after 20 July.

core eddy over succeeding weeks as a meander of the EAC formed and broke away from the shelf. Episodic catches continued around this point until 10–12 July (Fig. 2*centre* and see Fig. 5*b*).

On 10–12 July and again on 18–20 July there were episodes of high catch rates off Wollongong and Sydney (34.5°S), associated with cold doming that eventually pinched off the warm-core eddy (Fig. 2*centre* and see Fig. 5*b*). Episodes of high catch rates continued between Wollongong and Sydney (34–34.5°S) through 24–27 July, 30 July–1 August and 7–8 August, at the northern edge of the newly formed warm-core eddy (Fig. 2*right* and see Fig. 5*b*). During this period, high catch rates were recorded as shallow as 300 m and large quantities of running-ripe fish (>20% of females) were observed in some shots (Prince 1996).

1997

By May 1997 a large warm-core eddy had pinched off from the EAC and become a stable feature off Bermagui (36.5°S). During June the EAC was separating from the shelf around 33°S. The first episode of commercial catches began about 20 June and involved relatively low catch rates around Tuross (36°S) on the inside of the warm-core eddy (Fig. 3*left* and see Fig. 5*b*).

In early July the EAC went south along the shelf to Jervis Bay (35°S), where the current headed offshore forming a front. The warm-core eddy remained relatively stationary, moving slightly inshore and south. Catch rates around 36°S on the inside of the eddy increased and low catch rates were reported around Cape Howe 37°S on the leading edge of the eddy (Fig. 3*left* and see Fig. 5*b*).

Peak catch rates for the season were recorded on 13 July close to Jervis Bay (35°S) at the detachment point of the EAC (Fig. 3*centre* and see Fig. 5*b*). Single-pass SST imagery showed the largest catches to be clustered around the intensified main front (18–22°C) of the EAC. On 15 and 16 July a cold plume of water was evident immediately to the north of the survey catches (Prince *et al.* 1997). Lower catch rates (Fig. 5*b*) were also reported on that day, straddling the main surface front (17–22°C) of the EAC between Bermagui (36.5°S) and Wollongong (34.5°S).

Subsequently, the EAC pushed further south, gemfish catches declined and contracted to the south, with small catches continuing during the first week of August below the warmer surface water (Fig. 3*right* and see Fig. 5*b*).

1998

By April 1998 the main flow of the EAC was detaching from the shelf between Sydney (34°S) and Jervis Bay (35°S), forming a front that angled away from Sydney to the south-east out into the Tasman Sea (Fig. 4*left* and see Fig. 5*b*). This front appeared as a ‘cold ridge’ in the 250 m isotherm charts and it remained a semi-permanent and relatively stationary feature of 1998. Ultimately, the peak of gemfish catch rates occurred around the point at which the ridge intersected the shelf.

During April the EAC surged south of the ‘ridge’, a primary warm-core eddy pinched off near Cape Howe

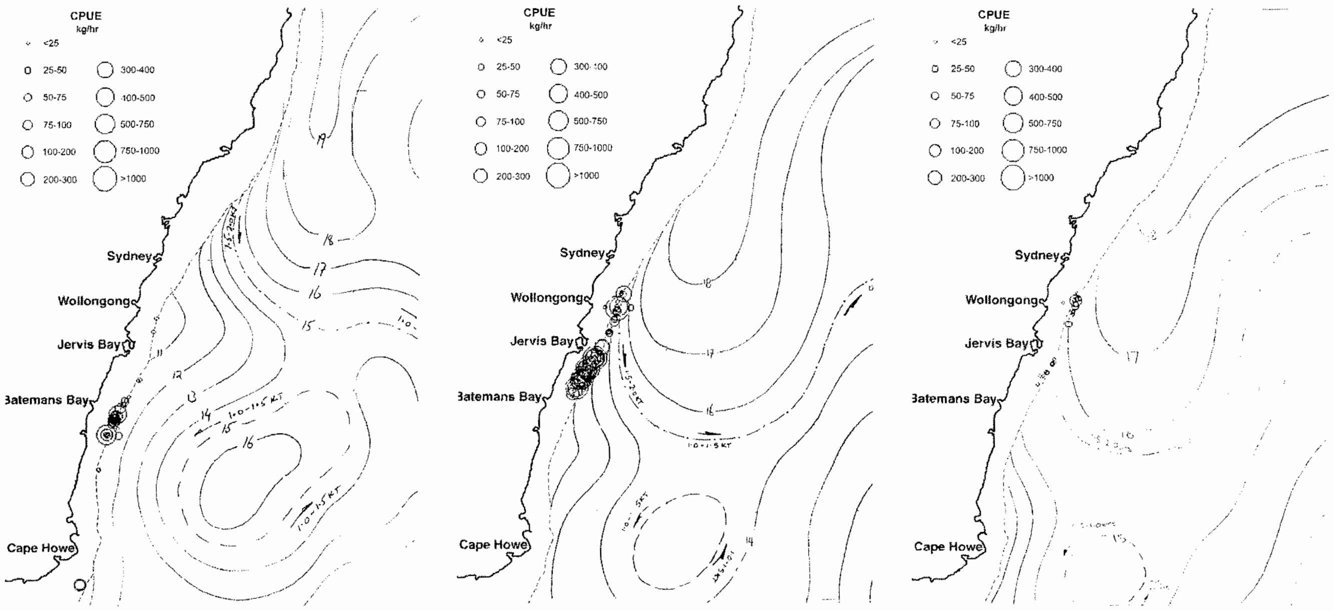


Fig. 3. METOC 250 m isotherm charts for winter 1997 overlaid with gemfish catch rates (kg h^{-1} by shot) observed during the 1997 industry survey (Prince *et al.* 1998*b*): *(left)* 25 June with catch data up to 8 July, *(centre)* 23 July with catch data 10-26 July and *(right)* 6 August with catch data post 27 July.

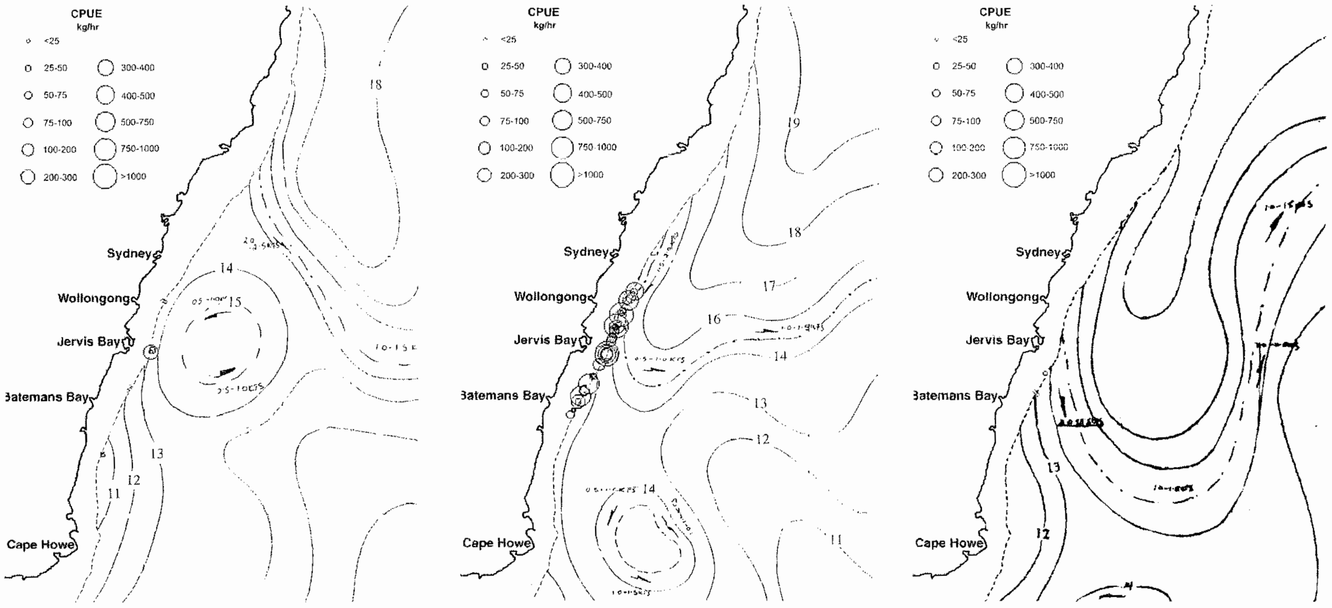


Fig. 4. METOC 250 m isotherm charts for winter 1998 overlaid with gemfish catch rates (kg h^{-1} by shot) observed during the 1998 industry survey (Prince *et al.* 1999): *(left)* 24 June with catch data up to 30 June, *(centre)* 22 July with catch data 1–26 July and *(right)* 19 August with catch data after 26 July.

(37.5°S) and the detachment point of the EAC returned to around Jervis Bay (35°S). During May the process repeated and a secondary warm-core eddy formed along the shelf between Tuross (36°S) and Eden (37°S), while the primary eddy weakened, and moved slightly offshore.

By late June 1998 (Fig. 4*left* and see Fig. 5*b*) the detachment point for the main flow of EAC was around Newcastle (33°S) and the main front angled south-east to level with Jervis Bay (35°S). The primary warm-core eddy was centered south of Lakes Entrance (38°S) and the secondary eddy was centered off Wollongong (35.5°S). A first small pulse of commercial catches was recorded at the end of June at the northern edges of both the primary (Cape Howe 37°S) and secondary eddies (Jervis Bay 35°S).

By 8 July (Fig. 4*centre* and see Fig. 5*b*) the EAC detached from the shelf north of Newcastle (32°S) was shown flowing south just seaward of the shelf break down to around Jervis Bay (35°S). Off Jervis Bay it flowed directly out to sea, forming the main front almost exactly where it had been at the end of April. A second episode of gemfish catches occurred during 5–8 July along the northern edge of both primary (Cape Howe 38°S) and secondary eddies (Tuross 36°S). During this episode, catches also straddled the main surface front (17–22°C) of the EAC at Wreck Bay (35.3°S), Shoalhaven (34.8°S) and, to a lesser extent, off Wollongong–Sydney (34.5°S) (Prince *et al.* 1998*a*).

A third pulse of gemfish catches and the peak catch rates for the season apparently came from a single mobile aggregation 13-19 July (Fig. 4*centre* and see Fig. 5*b*). During this period the centre of the aggregation moved steadily north from Wreck Bay (35.3°S) across the Shoalhaven grounds, and then over the Wollongong–Sydney grounds (34.5°S). Single-pass SST imagery showed the catches at this time to be associated with a cold eddy generated around the separation point of the EAC (Prince *et al.* 1998*a*).

The survey vessels lost contact with the aggregation just to the south of Sydney (34°S) when the gemfish moved off the trawl grounds onto an untrawlable area known as the ‘dumping grounds’ at the northern edge of the SEF. The few research catches after 26 July were small and comprised principally immature sub-adult gemfish (Fig. 4*right*).

Single-pass SST imagery showed that the separation point of the EAC generated successive cold eddies off Sydney (33.5–34°S) during 20 July to 10 August. Anecdotal reports from NSW state-licensed royal red prawn fishers operating to the north of the ‘dumping grounds’ suggest that the aggregation remained just to the north of Sydney until at least the beginning of August (Prince *et al.* 1998*a*).

The detachment point of the EAC remained off Sydney (34°S) until 12 August, when it began surging south towards its southern summer position.

Hypothesis formulation

Observations collected through the industry surveys of 1996–98 together with discussions with fishers suggested that gemfish aggregations form in predictable locations: firstly around the leading edge of the south-western edge of warm-core eddies interacting with the shelf break; secondly to the north, or north-west corner of warm-core eddies interacting with the shelf break; and finally the point at which the main flow of the EAC detaches from the continental shelf, around the northern limit of its seasonal cycle.

Knowledge of regional oceanography suggests that these are locations in which conditions favour the upward mixing of deep water at the shelf break (Pearce and Boland 1982; Huyer *et al.* 1988; Cresswell 1994).

SST imagery and SEF1 data

Mapping historic SEF1 data for 1987–98 against composite SST imagery allowed the claims of SEF fishers and our observations during the 1996–98 surveys to be tested to some extent.

Fig. 5 shows historic 10-day cloud-filtered composite SST imagery produced by the method of Walker and Wilkin (1998) for 1987–98 overlaid with the catch-rate data reported on SEF1 returns for those years. Episodic changes to fishery management regimes complicate interpretation of the SEF1 data to some extent. Closure of the fishery during July 1988 and low TACs or trip limits after 1990 all tend to mask natural influences on the data. The nature of the 10-day composite images also obscures much of the fine definition that examination of single-pass data suggested was important in determining the position of aggregations. However, the broad detail is still evident to some degree and the historic data confirm the observations made during the industry surveys of 1996–98.

During most winters, warm-core eddies form off the southern NSW shelf edge while the detachment point for the main EAC flow retreats towards its winter northern extreme between 30° and 35°S. Between late August and early October the EAC pushes back south through the study area towards its southern summer extreme.

As observed during the industry surveys of 1996–98, gemfish aggregations typically seem to form first on the southern edge of warm-core eddies interacting with the continental shelf (Fig. 5, 22 June 1987, 22 June 1989, 2 July 1991, 2 July 1992, 22 June 1996).

A second pulse of aggregations commonly forms on the north-west corner of warm-core eddies if they continue interacting with the shelf (Fig. 5, 12 July to 1 August 1987, 2 July 1989, 22 June 1990, 12 July 1991, 2 July 1992-12 July 1993, 12 July 1996, 12 July 1997).

The final pulse of aggregations forms around the actual point where the main body of EAC detaches from the continental shelf. This final pulse seems to coincide with the northern-most point reached by the detachment point during

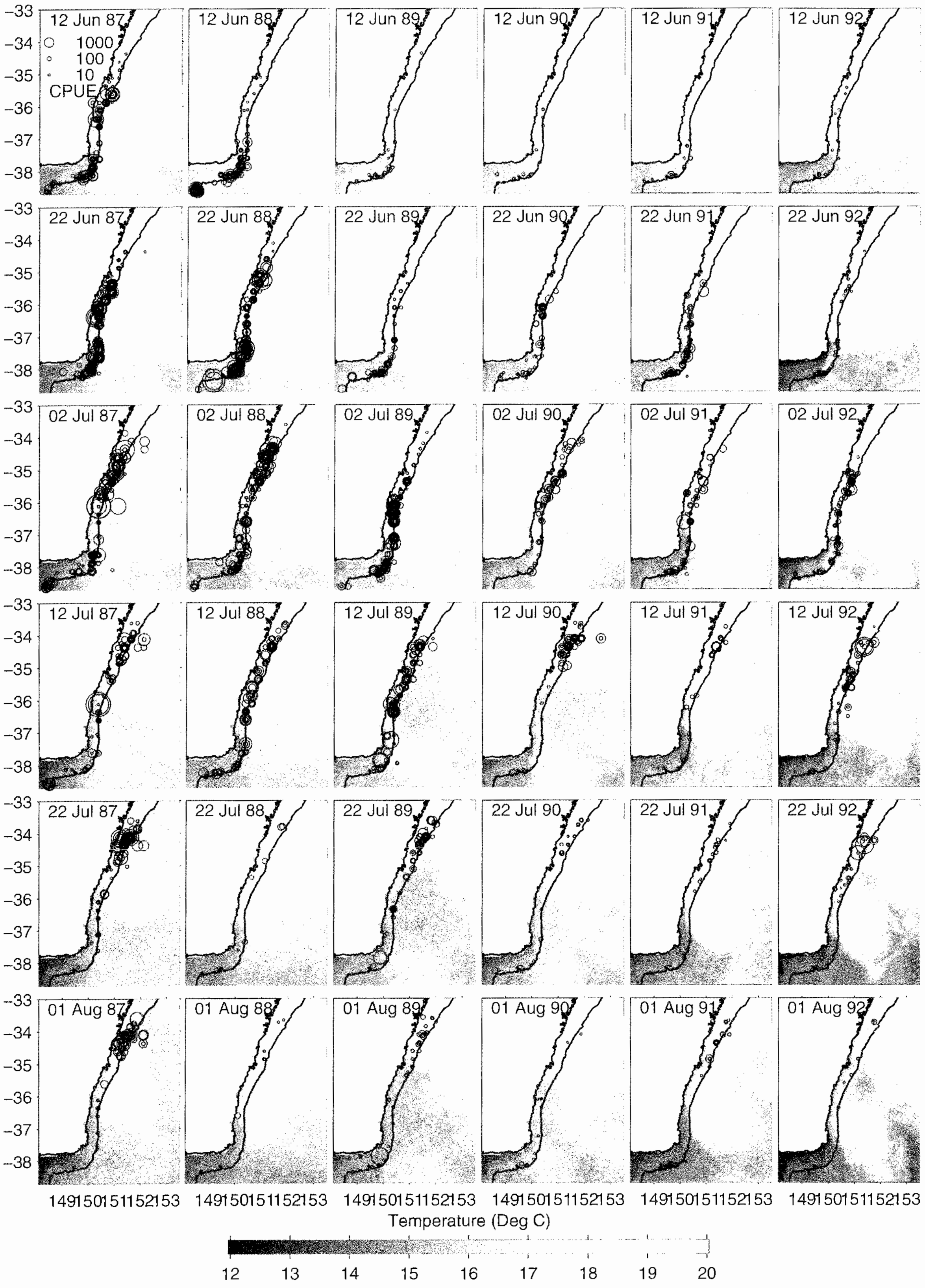


Fig. 5*a*. Catch rate (kg h^{-1} by shot) of gemfish reported on SEF1 logbooks overlaid on satellite estimates of sea surface temperature, for 1987–98. The date shown is the centre of the 10-day data window of both data types. The 500 m isobath is shown. Only half the available SEF1 catch data are shown prior to 1990, for clarity.

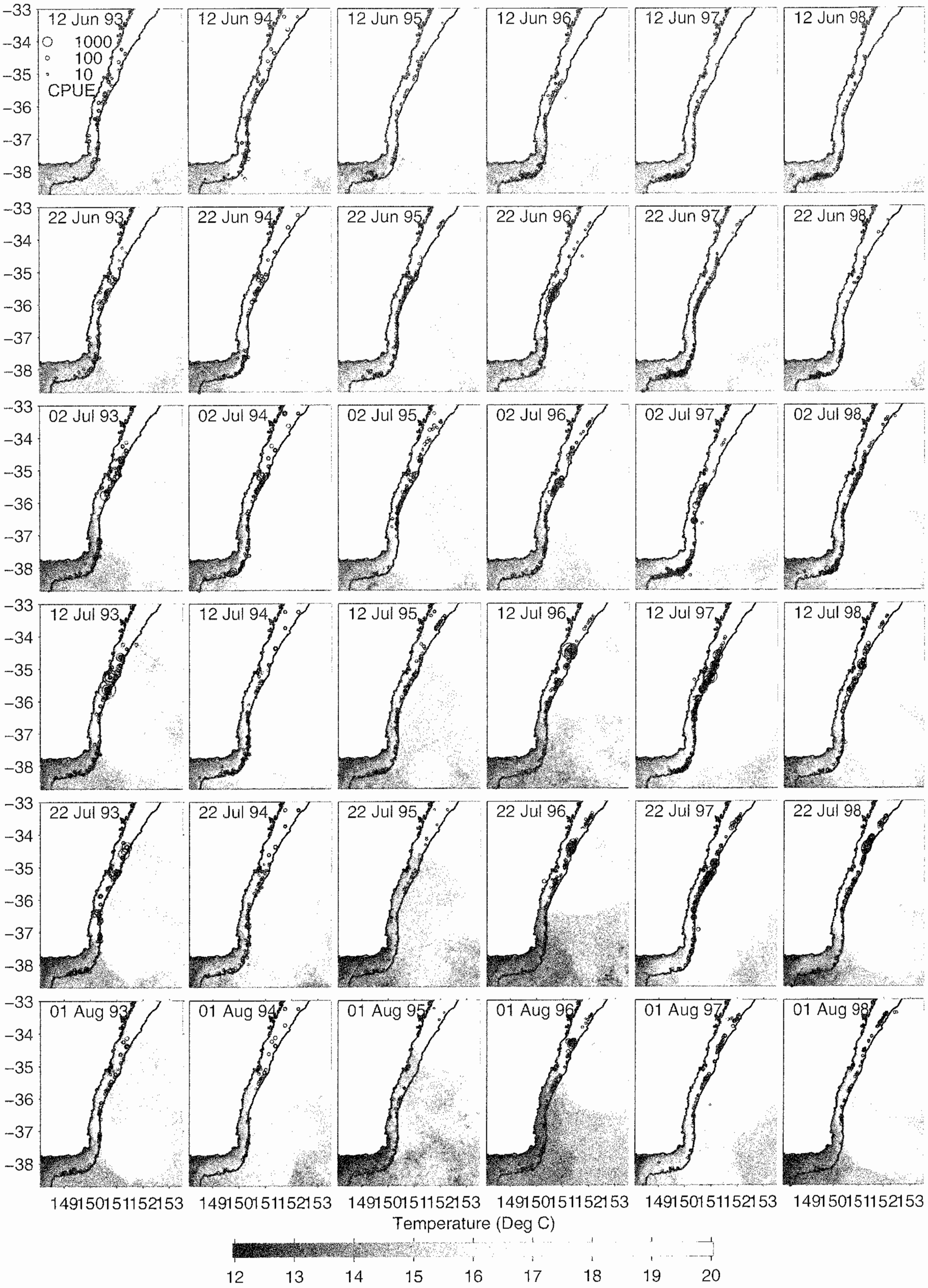

12 Jun 93
12 Jun 94
12 Jun 95
12 Jun 96
12 Jun 97
12 Jun 98
22 Jun 93
22 Jun 94
22 Jun 95
22 Jun 96
22 Jun 97
22 Jun 98
02 Jul 93
02 Jul 94
02 Jul 95
02 Jul 96
02 Jul 97
02 Jul 98
12 Jul 93
12 Jul 94
12 Jul 95
12 Jul 96
12 Jul 97
12 Jul 98
22 Jul 93
22 Jul 94
22 Jul 95
22 Jul 96
22 Jul 97
22 Jul 98
01 Aug 93
01 Aug 94
01 Aug 95
01 Aug 96
01 Aug 97
01 Aug 98
1000
100
10
CPUE
-33
-34
-35
-36
-37
-38
149150151152153
Temperature (Deg C)
12
13
14
15
16
17
18
19
20

Fig. 5*b*.

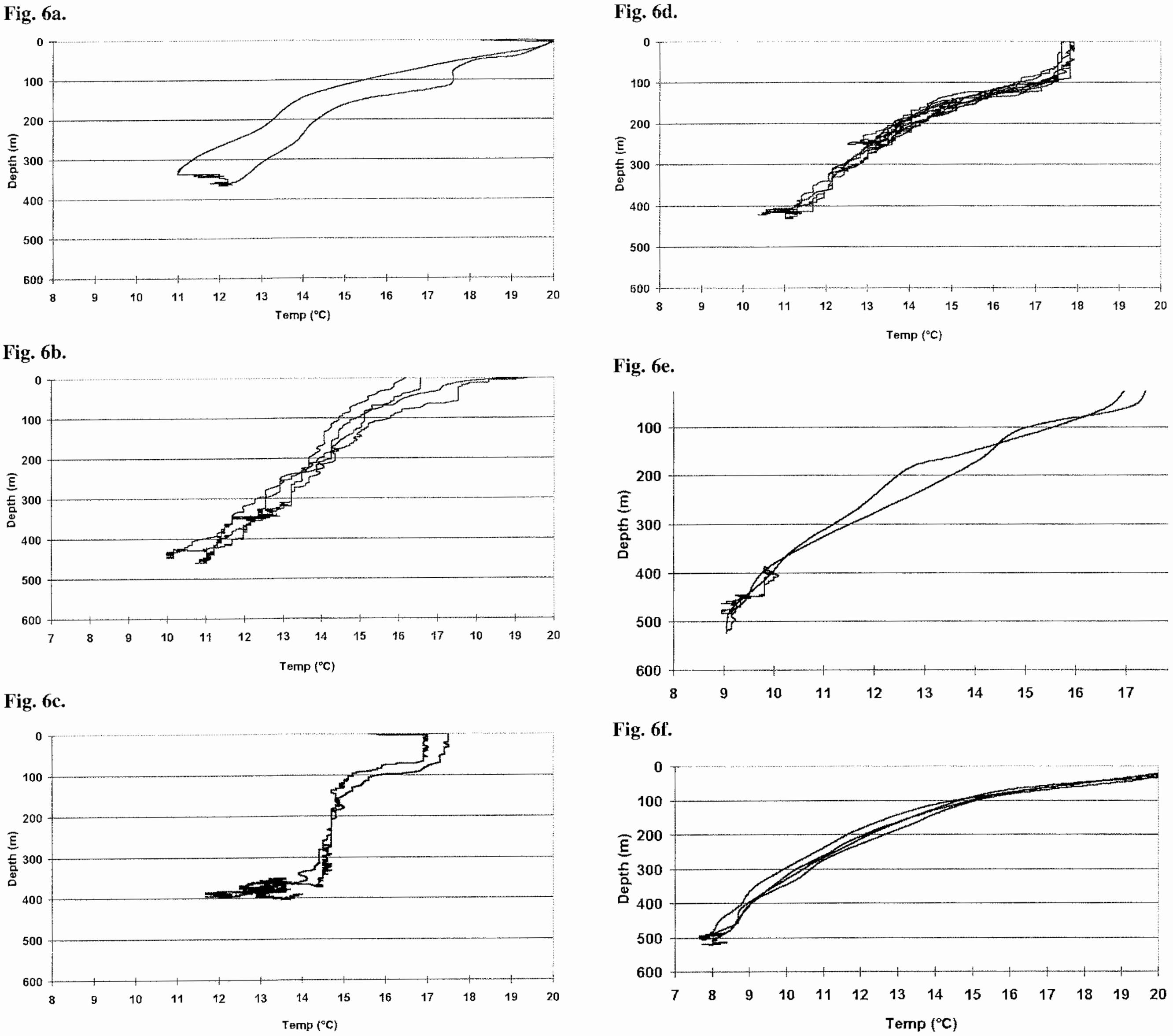


Fig. 6. Illustrative temperature and depth profiles: *(a)* Wollongong 14 July 1997, *(b)* Wollongong 12 July 1998 and *(c)* Ulladulla 11 July 1997 illustrate fronts typically observed when large gemfish catches were taken; *(d)* Wollongong 5 July 1998 and *(e)* Ulladulla 8 July 1997 show typical winter profiles prior to gemfish aggregations; and *(f)* Wollongong 12 January 1998 illustrates typical summer profile.

its annual cycle (Fig. 5, 12 July to 1 August 1989, 2–22 July 1990, 1 August 1991, 2 July 1994, 12 July 1995, 1 August 1996, 12–22 July 1997, 12–22 July 1998).

There is generally a close correlation between the main surface front (17–22°C) of the EAC and the location of gemfish aggregations in 400 m. This supports the fisher lore that gemfish catches are preceded by a rapid 2–5°C cooling of surface waters.

However, during the final phase of the season the aggregations appear not to be constrained by the surface front (Fig. 5, 22 July 1994, 22 July 1997, 22 July 1998). To some extent, this is explained by the composite nature of these SST images, which smoothes out much of the fine detail, but it is also indicative of the fact that the SST imagery shows only what is happening at the surface. Events at the surface are clearly linked with what is happening at 400 m where the gemfish aggregate, but the link is not a simple one. From the 250 m isotherm charts it appeared in 1997 and 1998 that when gemfish aggregations moved north of the surface front, at 250 m they were continuing to track the detachment point of the EAC.

Temperature and depth-profile data

As a final means of testing the supposition that gemfish aggregations are associated with deep mixing events at the shelf break, during the industry surveys of 1997 and 1998

Vemco temperature–depth recorders were deployed on the headlines of the trawl nets (Prince *et al.* 1997, 1998*a*). In addition, temperature and depth profiles were collected by one of the survey vessels operating out of Wollongong, at 34–35°S, throughout the period July 1997 to August 1998.

The temperature and depth profiles collected through 1997 and 1998 indicated that large gemfish catches were associated with 10–12°C water temperatures (Sub-Antarctic mode Water) and the presence of 1–3°C temperature fronts on the bottom. Successful gemfish shots were towed across fronts many of which extended through the entire water column. The existence of fronts was evidenced by a large temperature offset between the shooting away and retrieval of the nets (Figs 6*a* and 6*b*) or temperature variability at depth (Fig. 6*c*) during the shot. Compare Figs 6*a-c* (when gemfish catches were large) with Figs 6*d-f* (when gemfish catches were small).

The fact that fronts often extended throughout the water column explains why the aggregations of gemfish around 400 m can be often be tracked for much of the season by means of SST data.

Our measurements of seasonal temperature and depth profiles through the 34–35°S latitudinal band show that in general the winter gemfish season is characterized by temperature fronts and rapid cooling of the water column. Approaching summer, sea surface temperatures warm as the EAC resumes dominance and the temperature profile of the water column stabilizes, with temperatures decreasing smoothly with depth (Fig. 6*f*). No fronts or thermoclines were observed during the summer of 1997–98.

These observations support the supposition that winter gemfish aggregations are associated with ephemeral intrusion of Sub-Antarctic mode Water onto the shelf at the front of the EAC.

Discussion

Cushing (1974, 1975, 1982) has advanced the hypothesis that variation in the production of planktonic food for larval fish is a major determinant of recruitment variability in fish stocks. Under this hypothesis, it is not just the overall level of planktonic production that influences the survival of larval fish but also the degree to which the production of fish larvae in terms of timing and placement matches the production of the planktonic food sources. If this hypothesis is correct, we should expect strong evolutionary pressure to adapt spawning behaviour so that spawning and larval production is matched both spatially and temporally to the planktonic production that will sustain larval growth.

Our observations are that the winter aggregations of eastern gemfish coincide in space and time with ephemeral subsurface plumes of deep Sub-Antarctic mode Water that bathe this section of the continental shelf during later winter and spring and fertilize the water column. Hallegraeff and Jeffrey (1993) observed that phytoplankton blooms may also occur along this section of coast during summer, but that the autumn and spring blooms were larger and more predictable in timing; they postulated that these blooms would have a powerful influence on SEF fish stocks.

By selecting locations and times for spawning that coincide with subsurface pluming of Sub-Antarctic mode Water, gemfish could be ensuring that their planktivorous larvae are advected inshore with the enriching nutrients required to enhance phytoplankton production in the shelf environment (Tranter *et al.* 1986).

Acknowledgments

The industry-based surveys since 1993 have been financially supported by the South East Trawl Fishing Industry Association, the Fisheries Research and Development Corporation, the Fisheries Resources Research Fund and the Australian Fisheries Management Authorities Research Fund, and logistically supported by the fishers of the South East Trawl Fishery. We acknowledge the contributions of experienced fishers of eastern gemfish, now almost all retired. Also the support of our SEFAG colleagues and the field work of Messrs Geoff Diver and Stephen Rush.

References

Blaber, S. J. M., and Bulman, C. M. (1987). Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Marine Biology* **95**, 345–56.

Church, J. A., and Craig, P. D. (1998). Australia's shelf seas: diversity and complexity. In 'The Sea'. Vol. 11. (Eds A. R. Robinson and K. H. Brink.) (John Wiley: New York.)

Cresswell, G. (1994). Nutrient enrichment of the Sydney continental shelf. *Australian Journal of Marine and Freshwater Research* **45**, 677–91.

Cushing, D. H. (1974). The natural regulation of fish populations. In 'Sea Fisheries Research'. (Ed. F. R. Harden Jones.) pp. 399–412. (Elek Science: London.)

Cushing, D. H. (1975). 'Marine Ecology and Fisheries.' (Cambridge University Press: Cambridge.)

Cushing, D. H. (1982). 'Climate and Fisheries.' (Academic Press: London.)

Eastern Gemfish Assessment Group (2000). Eastern gemfish stock assessment. August 2000. (Australian Fisheries Management Authority: Canberra.)

Elliott, N. G., and Kloser, R. J. (1993). Use of acoustics to assess a small aggregation of orange roughy, *Hoplostethus atlanticus* (Collett), off the eastern coast of Tasmania. *Australian Journal of Marine Freshwater Research* **44**, 473–82.

Hallegraeff, G. M., and Jeffrey, S. W. (1993). Annually recurrent diatom bloom in spring along the New South Wales coast of Australia. *Australian Journal of Marine and Freshwater Research* **44**, 325–34.

Huyer, A., Smith, R. L., Stabeno, P. J., Church, J. A., and White, N. J. (1988). Currents off south-eastern Australia: results from the Australian Coastal Experiment. *Australian Journal of Marine and Freshwater Research* **39**, 245–88.

Johannes, R. E., Squire, L., Granam, T., Sadovy, Y., and Renguul, H. (1999). Spawning aggregations of groupers (Serranidae) in Palau. Marine Conservation Research Series Publication No. 1. (Nature

Conservancy www.tnc.org/asiapacific) 144 pp. (Nature Conservancy: San Francisco, CA.)

Koslow, J. A, Kloser, R., and Stanley, C. A. (1995). Avoidance of a camera system by a deepwater fish, the orange roughy (*Hoplostethus atlanticus*). *Deep-Sea Research* **42**, 233–44.

Neis, B., Schneider, D. C., Felt, L., Haedrich, R. L., Fischer, J., Hutchings, J. A. (1999). Fisheries assessment: what can be learned from interviewing resources users? *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1949–63.

Nillson, C. S., and Cresswell, G. R., (1981). The formation and evolution of East Australian Current warm core eddies. *Progress in Oceanography* **9**, 133–83.

Pankhurst, N. W. (1988). Spawning dynamics of orange roughy, *Hoplostethus atlanticus*, in mid-slope waters of New Zealand. *Environmental Biology of Fishes* **21**, 101–16.

Paulin, C. (1997). Lanternfishes: flashers of the deep. *Seafood New Zealand* February, 77–9.

Pearce, A., and Boland, F. M. (1982). Aanderaa current meter records from the New South Wales continental shelf, 1978–80. CSIRO Marine Laboratories Report No. 140.

Prince, J. D. (1996). Industry survey of the 1996 eastern gemfish spawning season. FRDC 96/157. (Biospherics Pty Ltd: PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D. (1999). Industry survey of the 1999 eastern gemfish spawning season. ARF 98/99–14. (Biospherics Pty Ltd: PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D., and Wright, G. (1994). A description of the size structure of the 1993 eastern Australian winter gemfish aggregations and a synthesis of industry's perspective on the existing stock assessment. FRRF 19/12 & FRDC 93/057. (Biospherics Pty Ltd: PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D., Griffin, D., and Diver G. (1997). Industry survey of the 1997 eastern gemfish spawning season. FRDC 97/147. (Biospherics Pty Ltd: PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D., Griffin, D., and Diver G. (1998*a*). Industry survey of the 1998 eastern gemfish spawning season. ARF 97/98–13. (Biospherics Pty Ltd: PO Box 168, South Fremantle, WA 6162, Australia.)

Prince, J. D., Baelde, P., and Wright G. (1998*b*). Synthesis of industry information on fishing patterns, technological change and the influence of oceanographic effects of SEF fish stocks. FRDC 97/114. (Biospherics Pty Ltd: PO Box 168, South Fremantle, WA 6162, Australia.)

Ridgway, K. R., and Godfrey, J. S. (1997). Seasonal cycle of the East Australian Current. *Journal of Geophysical Research* **102**, 22921–36.

Rowling, K. R. (1990). Changes in the stock composition and abundance of spawning gemfish *Rexea solandri* (Cuvier), Gempylidae, in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **41**, 145–63.

Rowling, K. R., Smith, D. C., Laurenson, F. A., Brown, L., and Broadhurst, M. (1990). Onboard observation of the 1989 gemfish fishery. Final Report, FIRDTF Project 88/126 (Fisheries Research Institute: Cronulla, Australia.)

Tomczak, M., and Godfrey, J. S. (1994). 'Regional Oceanography: an Introduction.' (Pergamon: Oxford.)

Tranter, D. J., Carpenter, D. J., and Leech, G. S. (1986). The coastal enrichment effect of the East Australian Current eddy field. *Deep Sea Research* **33**, 1705–28.

Walker, A. E., and Wilkin, J. L. (1998). Optimal averaging of NOAA/NASA Pathfinder satellite sea surface temperature data. *Journal of Geophysical Research* **103**, 12869–83.

Manuscript received 14 January 200; revised 31 October 2000;

Mar. Freshwater Res., 2001, **52**, 623–30

Comment on 'Spawning dynamics of the eastern gemfish (*Rexea solandri*) in relation to regional oceanography'

Kevin R. Rowling

NSW Fisheries, PO Box 21, Cronulla, NSW 2230, Australia

A comment on 'Spawning dynamics of the eastern gemfish (*Rexea solandri*) in relation to regional oceanography in south-eastern Australia' by J. D. Prince and D. A. Griffin, *Marine and Freshwater Research* **52**, 611–22.

Abstract. Temporal trends through the winter seasons in commercial landings of eastern gemfish (*Rexea solandri*) during the years 1977–79, 1982–85, 1986–87 and 1989–92 were reasonably stable for given latitudes, despite variable oceanographic influences, as depicted by 250 m isotherm data. This suggests that the overall pattern of occurrence of pre-spawning aggregations of eastern gemfish in these periods was determined by a combination of time of the season and latitude, rather than by oceanographic factors. Between 1986 and 1996, only four instances were identified where gemfish catches contained >10% of 'running ripe' females, and the variety of oceanographic conditions under which these catches were made provides little support for the hypothesis that eastern gemfish spawn into subsurface plumes of upwelled sub-Antarctic water.

Introduction

In their description of the factors affecting the location of pre-spawning aggregations of eastern gemfish (*Rexea solandri*), Prince and Griffin (2001) report observations from targeted research trawls conducted since 1996. These observations, and data on locations of commercial catches since 1987, are compared with '250 m isotherm maps' and sea-surface temperature charts to determine which environmental factors may significantly influence the location and movement of gemfish aggregations. 'Anecdotal' information from fishers, and temperature–depth profile data obtained from some trawl shots during 1997 and 1998, are also presented. After discussion of these data and observations, the authors conclude that gemfish aggregations coincide in space and time with oceanographic conditions that produce intrusions of colder sub-Antarctic water into the warmer waters of the East Australian Current (EAC). Specifically, aggregations of gemfish were found to occur where warm-core eddies interacted with the continental shelf, and also in association with the 'point of detachment' of the EAC from the continental shelf. These oceanographic conditions were considered to result in upwelling of colder sub-Antarctic water at the shelf break. Prince and Griffin (2001) infer that spawning of eastern gemfish occurs into subsurface plumes of this nutrient-rich sub-Antarctic water.

The fishery for eastern gemfish targets a well defined winter migration of mature fish at depths of 350 to 450 m, between latitudes 40°S and 33°S on the continental slope off south-eastern Australia (Rowling 1990). For the major part of the fishery, most of the catch has been taken with demersal trawls targeting the pre-spawning migration, during the months of June and July. The fishery has been through three very different phases since it developed in the early 1970s. Prior to 1988 annual catches exceeded 3000 t, and fishing was virtually unregulated. Because of the very heavy landings made during a comparatively short season, market gluts were common, and most trawlers targeted the pre-spawning 'run' when the fish were on their local grounds. However, following indications of declining catch rates and mean fish size (Rowling 1987), catch control in the form of a Total Allowable Catch (TAC) was introduced in 1988. Initially, the TAC was implemented as a 'global quota' and the fishery was closed when the TAC had been caught. However, from 1989 the TAC was allocated as Individual Transferable Quotas (ITQs) to individual fishers in proportion to their catch histories of gemfish over a defined period.

Between 1989 and 1992, a series of poor cohorts recruited to the mature population of eastern gemfish, and annual catches declined rapidly to <1000 t. From 1993 to 2000, because of concern about the depleted status of the mature population of eastern gemfish, the fishery was subject to a zero TAC (with the exception of 1997 when a 1000 t TAC was set, following indications of improved recruitment). The research trawls described by Prince and Griffin (2001) occurred during this period.

In this paper I present data from several representative periods of the fishery between the late 1970s and the early 1990s. These data show a very consistent pattern in time and

10.1071/MF01041 1323-1650/01/040623

space of eastern gemfish catches, irrespective of the oceanographic influences in each period. The likely causes of this stable migration pattern are discussed in relation to the findings of Prince and Griffin (2001). Observations on the location and timing of spawning of eastern gemfish are also discussed.

Methods

During the 1970s and 1980s, records of the daily landings of the main species by individual trawlers were obtained from district fishermen's co-operatives, the NSW Fish Marketing Authority and fish processing establishments. Prior to 1980, gemfish were often gutted before landing, and gutted weights were converted to whole weights by multiplying by 1.15 (an approximate conversion factor). For the periods 1977–79 and 1982–85, consistent data on gemfish landings by a constant fleet of trawlers were obtained for the ports of Wollongong (eight boats) and Ulladulla (nine boats). For each winter season, gemfish landings by trawlers at each of these ports were aggregated on a weekly basis, for a set series of eighteen weeks from the end of May to the end of September (the first week included the period from 29 May to 4 June, the second week was from 5 June to 11 June , and so on until the eighteenth week, which covered the period 25 September to 1 October, inclusive).

From 1986, more detailed data on the timing and location of gemfish catches became available from a shot-by-shot logbook completed by vessel skippers in the South-east Trawl Fishery. Reported catches of gemfish by all trawlers were aggregated for the 34°S and 35°S latitude blocks, using the same eighteen-week strata as were used for the co-operative data. These two latitude bands contain the main fishing grounds fished by the Wollongong and Ulladulla trawlers, respectively. Data were aggregated for the winter seasons 1986 and 1987 ('good' gemfish seasons, prior to any management intervention) and for the seasons from 1989 to 1992, when catches were declining and ITQ management was in place. Data for 1988 were not used, because of distortion of fishing patterns caused by the application of a 'global' TAC during that winter season and the closure of the fishery through most of July.

All available logbook data on gemfish catches for the years 1986 to 1993 were also aggregated by 1° latitude band for each of the eighteen weeks of the winter season, to determine the temporal pattern of landings within each latitude stratum.

Oceanographic charts for the Western Tasman Sea showing the isotherms at 250 m depth (interpolated from limited data by Royal Australian Navy METOC Services) were obtained from the Australian Oceanographic Data Centre, for the winter seasons from 1982 to 1993.

Finally, the time and location of all reported observations of significant levels of 'spawning females' (>10% of the catch of females) of eastern gemfish were noted, for comparison with oceanographic charts.

Results

Temporal distribution of gemfish landings in the Ulladulla and Wollongong areas

During the three winter seasons from 1977 to 1979 the seventeen trawlers from Ulladulla and Wollongong recorded total landings of 4707 t of gemfish. The temporal pattern of landings at each port (Figs 1*a* and 1*b*) showed a period of heavy catches from mid June to mid July (Weeks 3 to 7), and a secondary peak in landings in late August and early September (Weeks 14 and 15). Catch sampling showed that fish in the second period were spent, having spawned during the period of low catches in late July and August, presumably in a location where they were unavailable to vessels fishing from these ports. In 1977 and 1979, catches during the post-spawning period amounted to 13% and 12% respectively of the season's landings. However, in 1978, post-spawning catches were very heavy, with nearly 900 t of gemfish (47% of landings for the whole winter season) being landed during Weeks 14 and 15 by the seventeen vessels in the 'constant' fleet.

During the four winter seasons from 1982 to 1985 the same seventeen trawlers from Ulladulla and Wollongong recorded total landings of 3570 t of gemfish. The temporal pattern of landings at each port (Figs 1*c* and 1*d*) was similar to that found during 1977–79, the main difference being that the relative quantities landed during the post-spawning period declined, to average just 7% (range 5–11%) of total gemfish catches during these four seasons. Landings during the pre-spawning period showed the same temporal pattern in each of these areas as occurred during the 1977–79 period.

The temporal distribution of catches totalling 3845 t of gemfish reported in SEF logbooks for latitude blocks 34°S and 35°S during 1986 and 1987 again showed that a very high proportion of the catch (90%) was taken during the pre-spawning period. Off Ulladulla (the 35°S latitude block) the heaviest catches were again concentrated in a two-week period at the end of June and the start of July (Weeks 4 and 5), and off Wollongong (the 34°S latitude block) significant catches were taken throughout July, and small catches were taken during the post-spawning period (mainly Week 16 – Figs 1*e* and 1*f*).

A more restricted temporal distribution of gemfish catches was reported in SEF logbooks for these two latitude blocks for the period managed under ITQs (1989–92, Figs 1*g* and 1*h*). A total catch of 1599 t of gemfish was reported from these latitudes during this period, and again a high proportion of the catch in each season (average 86%, range 82–96%) was taken during the pre-spawning period. The main period of pre-spawning catches was relatively short in both areas, occurring in early July (Weeks 5 and 6) in the 35°S latitude block, and early to mid July (Weeks 6 to 8) in the 34°S latitude block.

Latitudinal pattern of gemfish landings through the winter season

When the reported logbook data on gemfish catches for all years from 1986 to 1993 were aggregated according to latitude and week of the winter season, the timing of the northward migration of pre-spawning gemfish could be clearly seen (Fig. 2). During these winter seasons, a reasonably tight distribution of catches occurred in the southernmost latitude blocks, with peak catches in Week 3 south of 38°S, Week 4 for the 37°S block, and Week 5 for

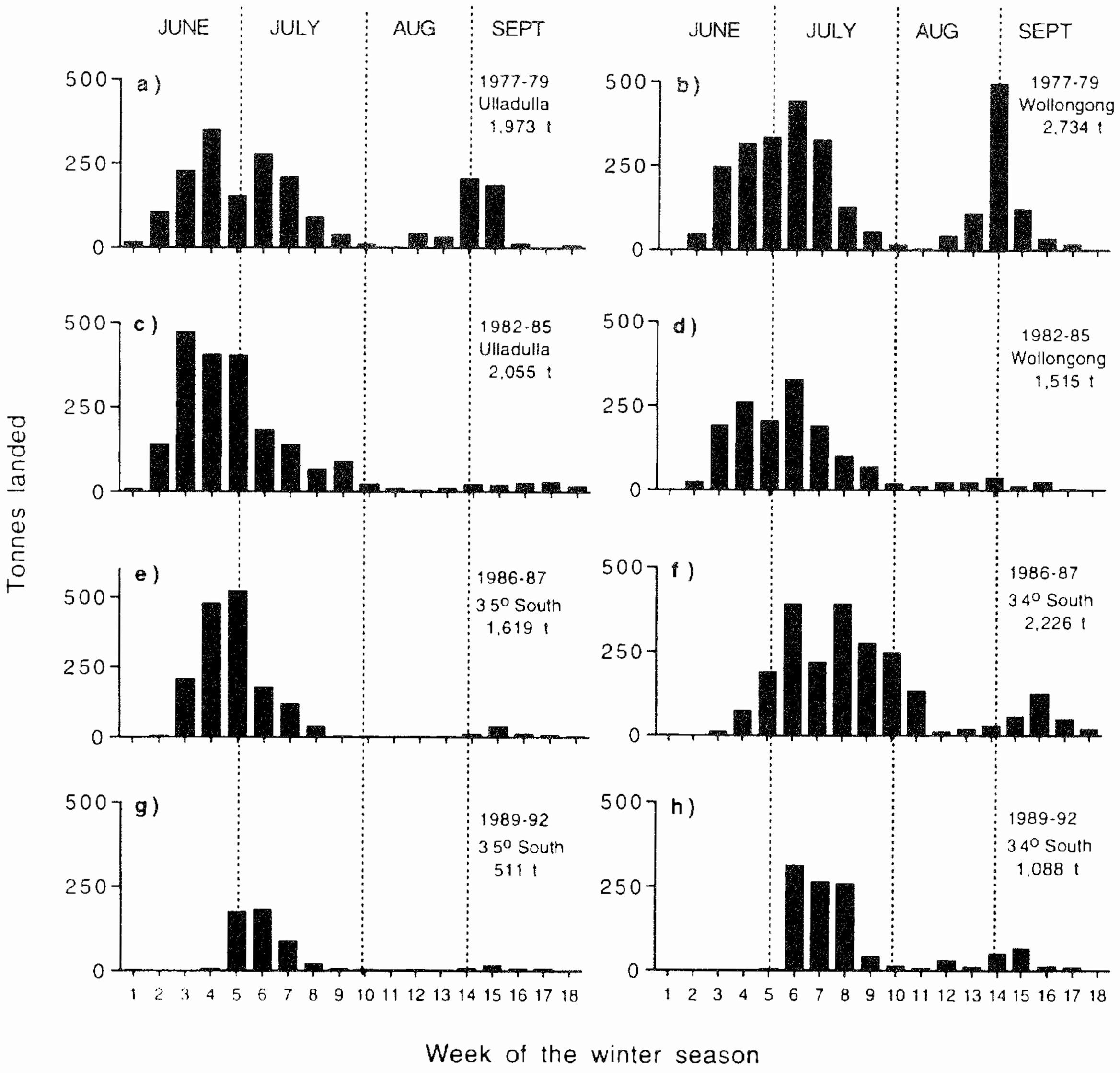


Fig. 1. Distribution of gemfish landings through the 18 weeks of the winter season (commencing 29 May) for the periods 1977–79 and 1982–85 from co-operative data for fixed fleets of trawlers at *(a, c)* Ulladulla and *(b, d)* Wollongong, and *(e–h)* for the periods 1986–87 and 1989–92 from SEF logbook data for all trawlers reporting catch from the 35°S and 34°S latitude blocks.

both the 36°S and 35°S latitude blocks. For fishing grounds north of 35°S, gemfish were caught throughout the July–September period, although the quantities reported were very low for grounds north of 33°S. Of the total winter catch of 13 817 t of gemfish recorded in logbooks between 1986 and 1993, 48% was reported from latitude blocks 34°S and 35°S.

250 m isotherm charts for the years 1982–93 (Fig. 3)

For most of these years, 250 m isotherm charts were available for the first week in July (which approximates the mid period of the pre-spawning 'run' of gemfish). However, for 1982, 1983, 1985 and 1987, charts were available only for late July or early August. These later charts are still considered to be indicative of oceanographic conditions during the pre-spawning period, because there are generally only minor variations in the patterns shown on the 250 m isotherm charts from week to week. The interannual variations in oceanographic pattern, as depicted by the 250 m isotherms, are clearly shown in Fig. 3. In general, the pattern during winter is for one or more warm-core eddies to be located off the NSW south coast; however, in some years warm-core eddies were not discernible (1990 and 1991) or appeared weak (1983, 1984 and 1989). Eddies were present, but not interacting with the continental shelf in 1982, 1985 (the southern eddy, centred on 38°S), and 1988 (the southern

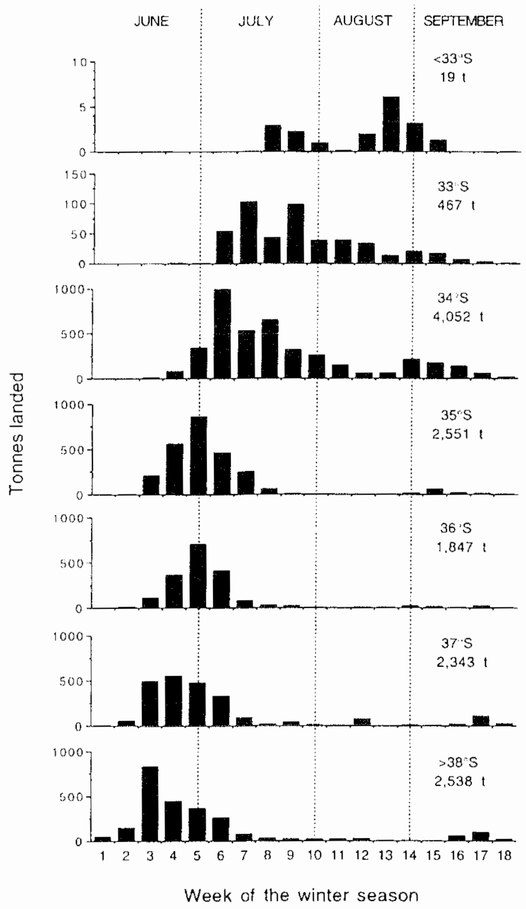


Fig. 2. Distribution of gemfish catches reported in SEF logbooks through the 18 weeks of the winter season (commencing 29 May) aggregated by 1° latitude bands, for all years from 1986 to 1993 combined. (Redrawn from Rowling 1997.)

eddy, at 38–39°S). The winter seasons from 1985 to 1988 provided examples of years when relatively strong warm-core eddies interacted with the continental shelf between latitudes 35°S and 37°S.

Observations of spawning events

Despite the fact that the fishery mainly targets pre-spawning aggregations of eastern gemfish, there have been relatively few catches where a high proportion of female fish have been observed to have ‘running ripe’ gonads. The recorded instances were:

- 1986, mid to late August : When a dropline fishery for gemfish first developed off Laurieton (31°39′S), catches were reported to contain a very high proportion of running-ripe females. These catches were taken just to the north of the main area of detachment of the EAC (Fig. 4*a*).
- 1992, 17–18 August : Significant landings of running-ripe fish were observed in catches from the Wollongong–Sydney area during sampling at the ‘Wollongong Fisheries’ processing plant. These catches were made from waters well south of the point of detachment of the EAC, which was near 33°S (Fig. 4*b*).
- 1993, 30 August – 2 September : Catches reported taken from waters ‘north of Sydney’ at the conclusion of the period of zero TAC (Prince and Wright 1994, p. 17) contained a high proportion of females in spawning condition. These catches were apparently taken from an area on the south-western edge of a warm-core eddy centred on 33°S, while the point of detachment of the EAC was well north of this at around 31°S (Fig. 4*c*).
- 1996, 30 July : Catches taken in the Wollongong area were reported (Prince 1996, p. 27) to contain a high proportion of females in spawning condition. These catches were taken from an area on the north-west corner of a warm core eddy centred between 35° and 36°S (Fig. 4*d*).

Discussion

The catch data indicate a very stable latitudinal pattern in the annual pre-spawning migration of eastern gemfish from the 1970s to the 1990s. If gemfish were aggregating mainly in response to oceanographic factors as suggested by Prince and Griffin (2001), these factors would also have been expected to exhibit a reasonably stable pattern in time and space. The 250 m isotherm data show considerable variation in the oceanographic patterns over this period (Fig. 3). It is therefore questionable whether oceanographic conditions represent the main influence determining the location and movements of pre-spawning aggregations of eastern gemfish. However, given that the overall pattern of aggregation and migration of mature gemfish appears to be determined by latitude and time of the winter season, the oceanographic factors raised by Prince and Griffin (2001) and other factors cited by commercial fishers (lateral current shears) may influence the day-to-day behaviour of gemfish aggregations on a local scale, and determine where good catches may be taken within latitude bands at a given time of the season.

In the early years of the fishery, the commencement of formation of the gemfish aggregations occurred at the same time each year (early June), suggesting that the behaviour is triggered by shortening day length as the winter solstice approaches. The average pattern of migration with latitude was also very similar between years (and remained so as the population declined significantly in the early 1980s, and through a further decline during the 1990s), suggesting a strong ‘latitudinal’ component in the migration (although it is unknown whether gemfish can detect changes in latitude). Such a pattern could also result from a combination of timing of migration and geography, if the main aggregations formed in the waters of eastern Bass Strait at about the same time each year, and proceeded generally northward along the edge of the continental shelf at some ‘average’ speed.

Stock assessments (EGAG 2000) found that the mature population of eastern gemfish had declined to around 35–

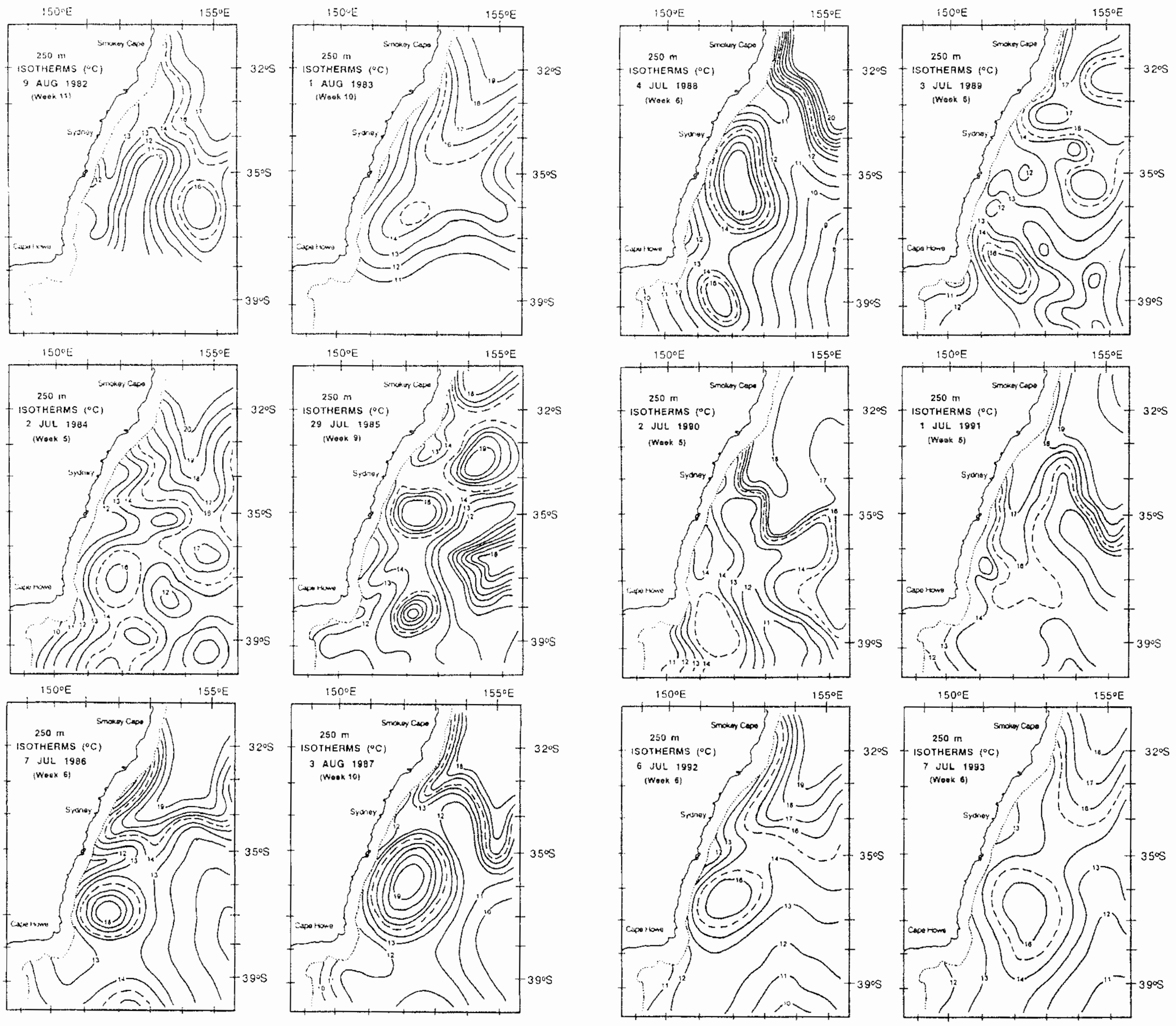


Fig. 3. Oceanographic conditions of the western Tasman Sea, as depicted by 250 m isotherm charts for the week ending on the date specified, for the winters from 1982 to 1993. Dotted line: approximate edge of the continental shelf. Dashed line: arbitrary boundary between 'Coral Sea' and 'Tasman Sea' water (15°C at 250 m depth). The appropriate 'week of the winter season' is also indicated.

40% of its unexploited level by the mid 1980s, presumably as a result of the effects of fishing. It was the predictable migration pattern of the pre-spawning aggregations of eastern gemfish that enabled the fishery to so effectively target the species in the late 1970s and early 1980s, before 'real time' information on sea surface temperatures or oceanography became generally available. Even in recent years, the use of oceanographic data by fishers targeting gemfish has been very limited. For example, during the industry survey of the 1996 spawning season when vessels engaged in the survey were asked to target pre-spawning aggregations within defined latitude bands, a considerable amount of time was spent in 'searching' for gemfish aggregations, despite the availability of data on sea surface temperatures and the 250 m isotherm. The vessel skippers '*often remarked that they were using several days of good weather to find the gemfish aggregations ...*' (Prince 1996, p. 9). If the aggregations were thought to be '*clearly associated with oceanographic conditions likely to have been causing upwellings*' (Prince 1996, p. 34), then with the oceanographic data available, more effective targeting of the aggregations should have been possible. It is worth

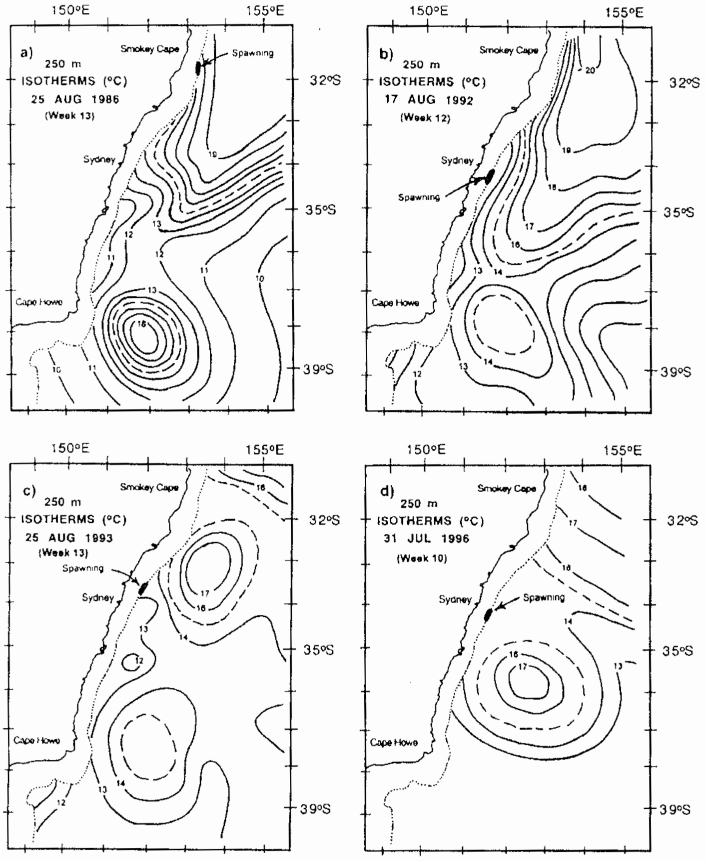


Fig. 4. Oceanographic conditions of the western Tasman Sea, as depicted by 250 m isotherm charts, for periods when relatively high proportions of spawning gemfish were observed in catches. The appropriate 'week of the winter season' is also indicated.

comparing the periods of highest catch rates during the 1996 survey (Prince 1996, p. 34) with the latitudinal patterns shown in Fig. 2:

25–27 June (Weeks 4–5 of the winter season) off Ulladulla (35°S latitude band)

10–12 July (Week 7 of the winter season) off Wollongong (34°S latitude band)

24–26 July (Week 9 of the winter season) again off Wollongong.

Although Prince (1996) observed that these latter catches off Wollongong '*occurred on the northern edge of a developing warm core eddy*' (see Fig. 4*d*), it is also true that all the periods of high catch rates observed during the 1996 industry survey fit exactly into the expected latitudinal migration pattern shown in Fig. 2.

The contention by Prince and Griffin (2001) that gemfish aggregations form where warm-core eddies interact with the continental shelf break is poorly supported by the evidence from years when this phenomenon has been observed. For example, in 1987 a strong eddy was centred at 35°S in June and had moved to 36°S by August, and was interacting with the shelf break throughout this period. Prince and Griffin claim that '*aggregations typically seem to form first on the southern edge of warm-core eddies interacting with the continental shelf (Fig. 5, 22 June 1987...)*'. However, the commercial catch data presented in their fig. 5 clearly show that very significant gemfish catches were taken in the 37°S and 38°S latitude blocks during early June, well south of the effects of the eddy. This same pattern of catches was repeated in 1988, when another strong eddy was interacting with the shelf break at 35°–36°S, and a weaker eddy centred on 39°S was not strongly interacting with the shelf break. When the commercial fishery for gemfish was closed on 10 July 1988 owing to the filling of the 3000 t competitive TAC, there were reports of good catches of gemfish (>3 t per shot, and representative of aggregations) on all grounds from south of Eden (38°S) to Wollongong (34°S). This widespread nature of the aggregations in early July 1988 was repeatedly cited by industry as being indicative of a large stock of gemfish, in their attempts to have the fishery closure lifted. (It should be noted that the widespread occurrence of aggregations on 10 July, which is the first day in Week 7 of the standard 18 weeks of the winter season, is consistent with the pattern presented in Fig. 2.)

In discussion of their results, Prince and Griffin (2001) infer that spawning of eastern gemfish coincides with oceanographic conditions that produce '*subsurface pluming of Sub-Antarctic mode Water*'. However, little evidence of where gemfish may be spawning is presented in the paper. Observations of 'spawning' gemfish have been few in the history of the fishery. In fact, female gemfish in 'running-ripe' condition were not observed in trawl catches until the mid 1980s (Rowling 1999), and there have been only four instances reported where catches contained a relatively high proportion (>10%) of running-ripe females. The variety of oceanographic conditions under which these catches were made provides little support for the hypothesis that gemfish actually spawn into subsurface plumes of upwelled water. However, all the observations of spawning occurred between Weeks 10 and 13 of the winter season and in areas to the north of about Wollongong (34°25′S), which reinforces the general observation that gemfish migrate north to spawn so that their larvae can take advantage of the higher productivity resulting from phytoplankton blooms and the associated zooplankton swarms that occur in latitudes 32°–34°S during spring (Hallegraeff and Jeffrey 1993). Just why gemfish is the only SEF species that appears to undertake such a directed migration to spawn in the northern part of its range remains a mystery. Oceanographic information analysed to date has also failed to explain why recruitment of gemfish was very poor from spawnings in all years from 1985 to 1989, improved considerably in 1990, was fair in 1991, and then returned to very poor levels from 1992 to 1995. Resolution of this question may provide insight into the environmental conditions that most influence the spawning dynamics of eastern gemfish.

References

EGAG (2000). Eastern gemfish stock assessment, August 2000. Report to the South East Fishery Assessment Group (SEFAG), South East Trawl Management Advisory Committee (SETMAC), South East Non-Trawl Management Advisory Committee (SENTMAC) and SEF Total Allowable Catch (TAC) Sub-Committee from the Eastern Gemfish Assessment Group (EGAG). (Australian Fisheries Management Authority: Canberra.)

Hallegraeff, G. M., and Jeffrey, S. W. (1993). Annually recurrent diatom blooms in spring along the New South Wales coast of Australia. *Australian Journal of Marine and Freshwater Research* **44**, 325–34

Prince, J. D. (1996). Industry survey of the 1996 eastern gemfish spawning season. Final Report, FRDC Project No. 96/157 (Biospherics: South Fremantle: Australia.)

Prince, J. D., and Griffin, D. A. (2001). Spawning dynamics of the eastern gemfish (*Rexea solandri*) in relation to regional oceanography in south-eastern Australia. *Marine and Freshwater Research* **52**, 611 – 22.

Prince, J. D., and Wright, G. (1994) A description of the size structure of the 1993 eastern Australian winter gemfish aggregations and a synthesis of industry's perspective on the existing stock assessment. Final Report, FRRF Project No. 19/12 and FRDC Project No. 93/057 (Biospherics: Leederville, Australia.)

Rowling, K. R. (1987). The need for catch controls in the gemfish fishery. NSW Fisheries Research Institute, Internal Report No. 26, June 1987 8pp. (NSW Dept Agriculture: Cronulla, Australia.)

Rowling, K. R. (1990). Changes in the stock structure and abundance of spawning gemfish *Rexea solandri* (Cuvier), Gempylidae, in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **41**, 145–63.

Rowling, K. R. (1997). The collapse of the eastern Australian gemfish stock – issues for management and the role of fisheries science. In 'Developing and Sustaining World Fisheries Resources : the State of Science and Management'. Proceedings, 2nd World Fisheries Congress, Brisbane, 1996. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. P. Beumer.) pp. 210–14. (CSIRO Publishing: Melbourne.)

Rowling, K. R. (1999). The fisheries biology and population dynamics of gemfish *Rexea solandri*. PhD Thesis, University of New South Wales, Sydney.

Manuscript received 14 March 2001

Reply

Jeremy D. Prince[A] *and David A. Griffin*[B]

[A]Biospherics P/L, PO Box 168, South Fremantle, WA 6162, Australia
[B]CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia

The phenomenon known as the 'gemfish run' is undoubtedly complex, and data relating to it are relatively sparse. Hence, present understanding of the phenomenon can be only rudimentary at best. Nevertheless, the fishery must be managed, so it is important that what is known about the fishery, or even *thought* to influence it, be openly discussed in the literature in order to expedite progress. Hence, we welcome Dr Rowling's comments on our paper.

One possible reason for the slight difference in interpretation of the data is that Rowling has binned the catch-rate data into 110 km (1° latitude) bands, whereas we have worked with the data on a shot-by-shot basis. For information on the physical environment, we have augmented the broad-scale picture provided by the weekly RAN METOC T250 maps with frequent (several per day), detailed (either 5 km or 1 km resolution) sea surface temperature maps and *in situ* measurements of the water column. Rowling agrees that the physical environment follows a general annual cycle, but that the timing and location of eddies, and the position of the separation of the East Australian Current from the coast (thus forming the Tasman Front), are essentially random. We have presented data and fishers' observations supporting the hypothesis that the gemfish run is closely connected with the details of the ocean environment. We do *not* claim (as Rowling implies we do) that by knowing the physical environment, for example by accessing an SST image, a fisher can home right in on the fish. We do believe, however, that such knowledge gives a fisher an advantage. If this were false, why do so many fishers, world-wide, purchase imagery? For support of our view, readers are referred to a related series of technical reports cited in Prince and Griffin (this issue), where detailed colour plots are available.

Furthermore, we cannot agree with Rowling that 'gemfish is the only SEF species that appears to undertake such a directed migration to spawn in the northern part of its range'.

Prince (2001) notes that many SEF species apparently exhibit northward movement along the eastern shelf of the SEF during winter. The fishing pattern of the SEF fleet itself apparently tracks these movements and exhibits the same north–south seasonal oscillation as the Tasman Front. Off the NSW shelf a cursory examination of the gonadal status of other species in the gemfish assemblage suggests that at least the southern frostfish (*Lepidopus caudatus*) and mirror dory (*Zenopsis nebulosus*) exhibit similar northward winter spawning movements. To the south of the gemfish assemblage, blue warehou (*S. brama*) and even orange roughy (*Hoplostethus atlanticus*) apparently exhibit similar patterns of behaviour (D. C. Smith, personal communication).

Prince (2001) speculates that these movements all link to the seasonal phytoplankton bloom that occurs near the Tasman Front along the northern edge of the sub-tropical convergence during late winter and spring. This common movement pattern presumably has the shared purpose of maximizing larval survival by matching egg and larvae production with ephemeral blooms of phytoplankton. Cushing (1974, 1975, 1982) found that the production of planktonic food for larval fish is a major determinant of recruitment variability in marine teleost stocks. Harris *et al.* (1988) found primary productivity in the SEF waters to be linked to the El Niño–Southern Oscillation phenomenon, and Young *et al.* (1993) documented the enriching influence of the 1990/91 La Niña event.

On this basis Prince (2001) speculates that the recruitment anomalies in many SEF species, including gemfish, will eventually be found to correlate with La Niña events.

References

Cushing, D. H. (1974). The natural regulation of fish populations. In 'Sea Fisheries Research'. (Ed. F. R. Harden Jones.) pp. 399–412. (Elek Science: London.)

Cushing, D. H. (1975). 'Marine Ecology and Fisheries.' (Cambridge University Press: Cambridge.)

Cushing, D. H. (1982). 'Climate and Fisheries.' (Academic Press: London.)

Harris, G. P., Davies, P., Nunez, M., and Meyers, G. (1988). Interannual variability in climate in Tasmania, and its effect on freshwater and marine fisheries. *Nature* **333**, 754–7.

Prince, J. D. (2001). Ecosystem of the South East Fishery (Australia), and fisher lore. *Marine and Freshwater Research* **52**, 431–49.

Young, J. W., Jordan, A. R., Bobbi, C., Johannes, R. E., Haskard, K., and Pullen, G. (1993). Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern Tasmania, Australia. *Marine Biology* **116**, 9–18.

Mar. Freshwater Res., 2001, **52**, 631–6

Larval distribution and abundance of blue and spotted warehous (*Seriolella brama* and *S. punctata*: Centrolophidae) in south-eastern Australia

B. D. Bruce[A], *F. J. Neira*[B] *and R. W. Bradford*[A]

[A]CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia
[B]Australian Maritime College (AMC), PO Box 21, Beaconsfield, Tas. 7270, Australia

Abstract. The early life histories of the commercially important blue and spotted warehous (*Seriolella brama* and *S. punctata*) were examined on the basis of archived ichthyoplankton samples collected over broad areas of southern Australia. Larvae of both species were widely distributed during winter and spring within shelf and slope waters. Larvae of *S. brama* were recorded from Kangaroo Island, South Australia (SA), to southern New South Wales (NSW). *Seriolella punctata* larvae were recorded from western Tasmania to southern NSW. Back-calculated spawning dates, based on otolith microstructure, indicated that spawning predominantly occurs during late July and August but that the timing of spawning varies between regions. The abundances of small larvae (<5.0 mm body length) were highest for both species off western Tasmania and southern NSW. No small *S. brama* larvae were recorded between southern Tasmania and southern NSW, whereas low but consistent numbers of small *S. punctata* larvae were found between these regions. The data suggest that there are separate spawning areas for *S. brama* in western and eastern regions of Australia's South East Fishery. The pattern for *S. punctata* is less clear, but suggests a more continuous link among populations in south-eastern Australia.

Introduction

Blue warehou (*Seriolella brama*) and spotted warehou (*S. punctata*) are medium-sized fishes found primarily in shelf and upper slope waters of south-eastern Australia and in New Zealand (Gomon *et al.* 1994). Both are commercially important across their range and are two of the main quota species within the South East Fishery (SEF) of south-eastern Australia (Tilzey 1998). *Seriolella brama* and *S. punctata* are targeted by both the trawl and the non-trawl sectors of the SEF. They are caught as by-catch in the Southern Shark Fishery, and juvenile *S. brama* are often caught by recreational anglers in bays and estuaries (Kailola *et al.* 1993). Commercial catches of both species reach a seasonal peak in winter–spring, although there is marked interannual variability in catches, possibly linked to environmental factors (e.g. water temperature) that may affect catchability and recruitment (Tilzey 1998). Catch rates and total catches of *S. brama* declined over the mid 1990s in both the trawl and non-trawl sectors and this was accompanied by a substantial reduction in the mean catch-at-age in some sectors of the fishery (MacDonald and Smith 1996). These effects have led to concerns over the population status of blue warehou stocks in south-eastern Australia (Smith 1995).

Both species are assumed to be single stocks within the SEF. However, no formal analysis of stock structure has been undertaken and there is some uncertainty with the single stock model. Both are believed to be highly mobile species (Gavrilov and Markina 1979), although the results of tagging studies in south-eastern Australia have been inconclusive (Knuckey, personal communication). The relationship between populations to the west and east of Bass Strait, where the bulk of the commercial catch is taken, is unknown. In addition, uncertainty about the stock structure and the effects of fishing on the spawning populations has caused conflict between the various sectors of the industry (Knuckey and Sivakumaran 2001).

A recent study by Knuckey and Sivakumaran (2001) has provided information on the reproductive biology of *S. brama* and confirmed previous observations by Smith (1989) of a winter–spring spawning across south-eastern Australia. They also reported regional differences in the timing of spawning, with fish east of Bass Strait spawning approximately one month earlier than those west of Bass Strait. However, the actual locations of spawning for both *S. brama* and *S. punctata* are still unknown and they have not been documented for Tasmanian waters. Similarly, the early life history of both species is poorly known. Grimes and Robertson (1981) described the eggs and yolk-sac larvae of *S. brama* from New Zealand, whereas full developmental sequences of larvae for both species were only recently described (Bruce *et al.* 1998). Last *et al.* (1983) reported that small juveniles of both species are commonly found under scyphomedusae in bays and estuaries of south-eastern Tasmania.

10.1071/MF99150 1323-1650/01/040631

We report herein the distribution and occurrence of *S. brama* and *S. punctata* larvae in south-eastern Australia, based on the analysis of archived ichthyoplankton samples taken between 1984 and 1999. The data provide further details of the timing and location of spawning, as well as general aspects of the two species' early life history.

Materials and methods

Field sampling

In total, 6519 archived plankton samples from about 3000 stations collected between 1984 and 1999 were examined for the presence of *Seriolella* larvae. The available samples, covered a wide area of southern and south-eastern Australia (Fig. 1). Samples covered all seasons, including day and night tows, in shelf and open ocean areas, and were generally taken concurrently with hydrographic data. Most *Seriolella* larvae were retrieved from samples taken in 1984, 1985, 1986, 1993 and 1997.

Four net systems (surface, ring, Bedford Institute of Oceanography Net and Environment Sensing System [BIONESS] and bongo) were routinely used to collect samples, depending on the objectives of the original survey. Towing protocols and net types differed between systems and details are fully described in Bruce *et al.* (1996 and in press), Young *et al.* (1996) and Gunn *et al.* (1989). Net systems are briefly described below.

Surface net. The surface net consisted of a square frame with a mouth area of 1 m^2 and mesh size of 1000 µm. The net was towed beside the vessel from a davit rigged amidships and was usually deployed concurrently with other net systems towed astern or on departing a hydrographic station. The net in all cases was towed at a vessel speed of between 2.5 and 3.5 kn for 10–15 min.

Ring net. The ring net consisted of a circular framed net of 70 cm diameter and 500 µm mesh. This net was either towed amidships as a surface net, or towed obliquely from the stern through the water column at a vessel speed of 2.5–3.5 kn, the latter from within 10 m of the bottom (maximum depth 200 m) to the surface.

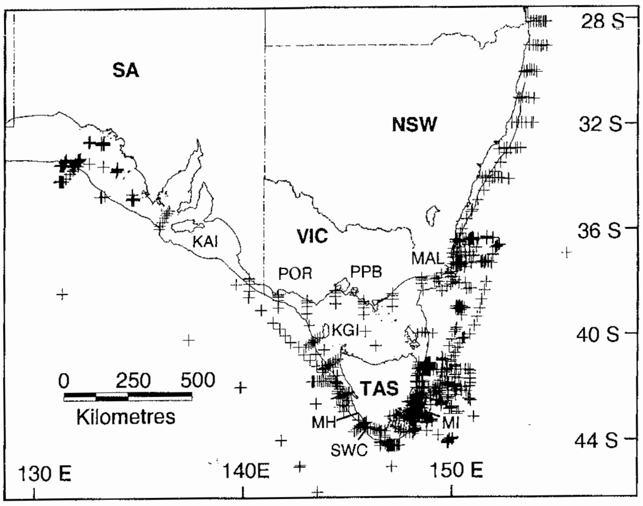


Fig. 1. Distribution of samples available for analyses of larval distribution in south-eastern Australia. NSW, New South Wales; VIC, Victoria; TAS, Tasmania; SA, South Australia; MAL, Mallacoota; PPB, Port Phillip Bay; POR, Portland; MI, Maria Island; SWC, South West Cape; MH, Macquarie Harbour; KGI, King Island; KAI, Kangaroo Island.

Bongo net. The bongo net consisted of two nets, each either 60 cm or 70 cm diameter, with a mesh size of either 1000 µm or 500 µm (depending on the study), and was towed from a central pivoting point. Bongo nets were towed either as a surface net or obliquely through the water column in a similar manner to the ring net. The depth of obliquely towed bongo nets was monitored in real time by sensors on the net relayed to the vessel via a conducting cable.

BIONESS net. The BIONESS net was used to examine vertical distribution. The BIONESS net consisted of a towed frame with a mouth opening of 1 m^2, fitted with up to 10 nets of either 335 µm or 500 µm mesh. Each net could be opened and closed from an on-board control system with communication between ship and net via a conducting tow cable. The tow cable also relayed real-time information to the vessel from sensors on the frame that provided net depth, rate of descent/ascent, elapsed fishing time and volume of water filtered. The system was towed from the stern of the vessel at a speed of about 3 kn. A typical tow profile consisted of deploying the sampler to the maximum depth and then sampling through discrete strata back to the surface. The maximum depth sampled and the resolution of depth strata varied according to water depth and, in some cases, the original target species. Most BIONESS tows were conducted seaward of the shelf break, where a typical tow profile consisted of an oblique set from the surface to 400 m over a 40 min period, followed by 10–20 min hauls from 400–300 m, 300–200 m, 200–100 m and 100 m to the surface.

A study during 1997 examined the vertical distribution of ichthyoplankton along the Victorian and south-eastern South Australian coasts on a series of eight fixed parallel transects between Gabo Island (37°36.0′S,149°55′E) and Port MacDonnell (37°49.0′S,140°17′E).

Each transect was located 65 nautical miles (nmiles) apart, and each contained five sampling stations at 2, 4, 8, 16 and 32 nmiles offshore. Sampling was conducted mostly during daylight hours. In stations where bottom depth was $\geq$100 m, discrete samples were obtained in the strata 100–75, 75–50, 50–25 and 25–0 m by the use of four 500 µm mesh nets. Each net was opened for 15 min while towing the BIONESS system obliquely at a speed of 1–2 kn. In stations <30 m deep, a 15 min oblique tow in the strata 25–0 m used the bongo sampler instead of the BIONESS net. Surface samples were also collected at each station in a bongo sampler described above. This study provided the best available information on vertical distribution.

The volume filtered was calculated for tows from each net system by the use of either Rigosha or General Oceanics flowmeters. Samplers were assumed to have the same filtration efficiency for the purpose of analyses. Day–night differences in the catchability of larvae have not been considered and the data have been standardized to numbers of larvae per 1000 m^3 for comparison.

Samples were fixed in either 10% formalin seawater buffered with sodium tetraborate or 98% ethanol (the latter for ageing).

Laboratory analyses and ageing of larvae

All *Seriolella* larvae were removed from the available samples and identified to species following the descriptions of Bruce *et al.* (1998). Body length (BL) was measured to the nearest mm (notochord length in preflexion larvae and standard length in flexion and postflexion larvae) under a dissecting microscope fitted with a calibrated eyepiece graticule, following the definitions of Neira *et al.* (1998).

Larvae of both *S. brama* and *S. punctata* were aged by examination of otolith microstructure that followed the procedure of Brothers *et al.* (1976). Increment formation was assumed to be daily, on the basis of the similarity of increment structure to that in species for which age validation has been previously documented (e.g. Jenkins 1987; Thresher *et al.* 1988), the concurrence of our back calculated spawning dates with documented spawning periods (Smith 1989; Knuckey and

Sivakumaran 2001), and the formation of increments in laboratory-reared *S. punctata* larvae (Bruce *et al.* 1996).

Increment counts were taken from whole, unprocessed sagittae mounted in a drop of lens immersion oil. Otoliths were examined under transmitted light at 1200–2500× under a Leitz Orthoplan microscope fitted with a high-resolution television camera (Ikegami CTC-6000) and linked to a high-resolution monitor. Increment age was estimated by averaging counts from both sagittae (where counts from a respective otolith set did not differ by >5%). Otolith pairs not satisfying these criteria were rejected from subsequent analyses (2.1%). Total age was estimated as increment age + 6 (based on the estimated period between fertilization and first increment formation for *S. punctata*; see Bruce *et al.* [1996] for details). Total age was used in all calculations of growth rate and in back-calculating spawning dates.

Otoliths from larvae collected between 1984 and 1986 had deteriorated and were unreadable, despite storage of specimens in 98% ethanol. Therefore we calculated age-at-length relationships from larvae collected in 1993 and whose otoliths were readable and in good condition. Growth in both species was essentially linear at sizes <7 mm BL and is best described by the following equations:

$$\begin{array}{lll} \textit{S. brama}: & [\text{age}] = 6.321[\text{BL}] - 18.71, & R^2 = 0.86; \\ \textit{S. punctata}: & [\text{age}] = 5.814[\text{BL}] - 17.32, & R^2 = 0.81. \end{array}$$

Age was estimated for a randomly selected subset of larvae that were collected between 1984 and 1986 and that were less than 7.0 mm BL from these equations.

The spawning date for each aged larva was calculated by subtracting total age from the date of capture.

Results

Regional distribution

In total, 695 *S. brama* larvae and 739 *S. punctata* were recorded from the available samples. Larvae of both species were widely but unevenly distributed across south-eastern Australia and were primarily restricted to shelf and slope waters. Very low numbers were recorded seaward of the slope and none was recorded from samples >25 km offshore of the shelf break (Fig. 2).

Seriolella brama. Larvae were recorded from Kangaroo Island in South Australia to southern New South Wales (Fig. 2). They were low in abundance in South Australian samples but increased in abundance eastwards towards Bass Strait. Low numbers were recorded within western Bass Strait as far east as Port Phillip Bay in Victoria.

Larvae were most abundant between King Island and South West Cape along the coast of western Tasmania, with the maximum abundances recorded between King Island and Macquarie Harbour. Larval abundance decreased eastwards around southern Tasmania and they were only recorded in extremely low numbers between Maria Island on the east Tasmanian coast and north-eastern Victoria. Large numbers of larvae were again recorded in a restricted area between Mallacoota in north-eastern Victoria and Bermagui in southern NSW.

The distribution of small preflexion larvae (<5.0 mm BL) was assessed separately to provide an indication of possible spawning areas. In general, the distribution of small larvae mirrored that of all larvae combined (Fig. 3). Small larvae were primarily recorded from Kangaroo Island to South West Cape in Tasmania and off southern NSW. Small larvae were absent from Bass Strait and only three small larvae were recorded between South West Cape (Tas.) and Mallacoota (Vic.). Small larvae were most abundant between King Island and Macquarie Harbour off western Tasmania.

Seriolella punctata. Larvae were less widely distributed than those of *S. brama.* Larval *S. punctata* were absent from samples taken north of Sandy Cape (western Tasmania) and from samples taken either west of or within Bass Strait (Fig. 2). They were recorded from western Tasmania to southern NSW. The highest abundances of larvae were recorded off south-western and southern Tasmania, and off north-eastern Victoria and southern NSW. Larvae were consistently recorded between Maria Island (eastern Tasmania) and north-eastern Victoria, although in low numbers.

The distribution of small preflexion larvae (<5.0 mm BL) again mirrored that of all sizes combined (Fig. 3). Small larvae were most abundant off southern Tasmania and north-eastern Victoria/southern NSW, with low but consistent numbers between these two regions.

Vertical distribution

Very few *Seriolella* larvae were recorded in vertically stratified samples. A sample set collected in Bass Strait recorded small numbers of *S. brama* larvae that were too few to warrant a statistical analysis. *Seriolella brama* larvae were recorded from the surface to the 75–100 m stratum, with the highest abundances in the upper 50 m (Fig. 4).

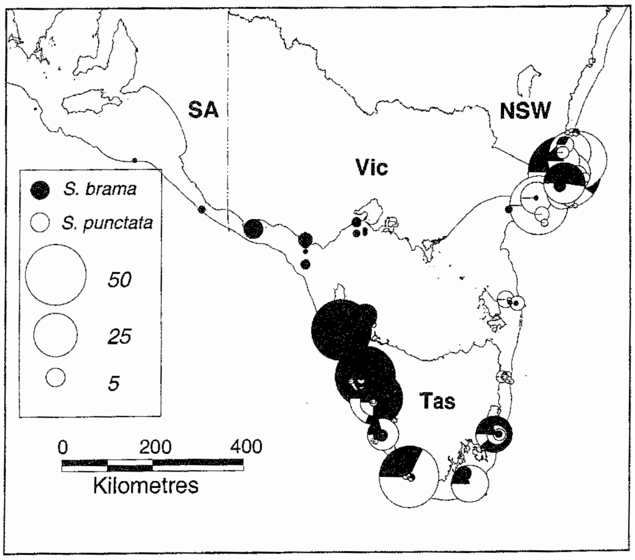


Fig. 2. Distribution of *S. brama* larvae and *S. punctata* larvae in southern Australia (all sizes combined). Scale, number of larvae per 1000 m^3.

Both *S. brama* and *S. punctata* were routinely recorded from surface tows in southern NSW. In addition, larvae as well as pelagic juveniles of both species were caught in association with scyphomedusae in surface waters of Storm Bay in Tasmania.

Age and growth

Larvae of both *Seriolella* species had a series of unambiguous bipartite increments extending from a central core to the edge in both sagitta.

Larvae used for ageing were taken from samples collected from 1993, and most were from specimens collected in both NSW and Tasmanian waters. *Seriolella brama* and *S. punctata* larvae used in ageing ranged from 2.9 to 18.6 mm (n = 34) and 2.8 to 12.0 mm (n = 165), respectively. Similar patterns of age and growth were recorded for each species and growth was best described by the following exponential equations over these size ranges.

S. brama: $[BL] = 3.2952e^{0.0303[age]}$, $R^2 = 0.85$;
S. punctata: $[BL] = 3.1736e^{0.0386[age]}$, $R^2 = 0.94$.

Back-calculated spawning dates

Back-calculated spawning dates indicated that spawning peaked in winter for both species. However, the range of spawning dates and timing of peak spawning varied between regions.

Seriolella brama. Spawning was recorded on 45 days over a 77-day period from 21 June to 6 September. Spawning dates for larvae collected from Tasmanian waters (primarily from the west coast) ranged from 5 July to 6 September, with a peak in mid to late August (Fig. 5). Spawning dates for larvae collected from north-eastern Vic./southern NSW ranged from 21 June to 8 August, with a spawning peak in late July, approximately one month earlier than that calculated from aged larvae caught in Tasmania.

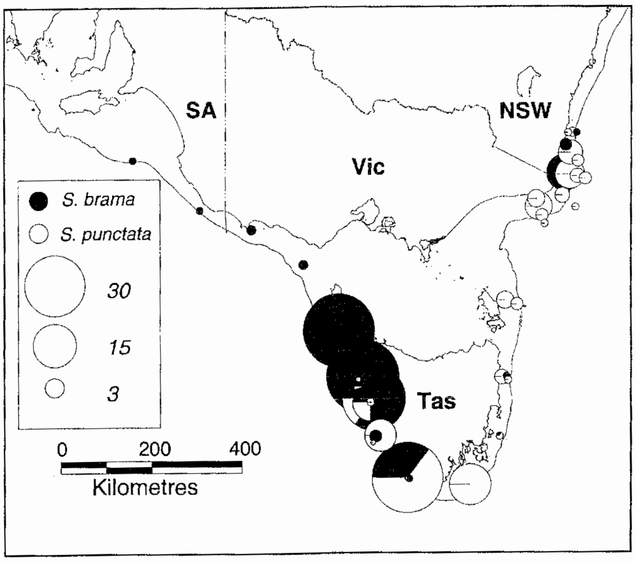


Fig. 3. Distribution of *S. brama* larvae and *S. punctata* larvae <5 mm BL. Scale, number of larvae per 1000 m^3.

Seriolella punctata. Spawning was recorded on 32 days over a 47-day period from 1 July to 17 August. Spawning dates for larvae collected from Tasmanian waters (primarily from the south coast) ranged from 18 July to 17 August, with a peak in early–mid August (Fig. 6). Spawning dates for larvae collected from north-eastern Vic./southern NSW ranged from 1 July to 11 August, with a spawning peak in late July–early August.

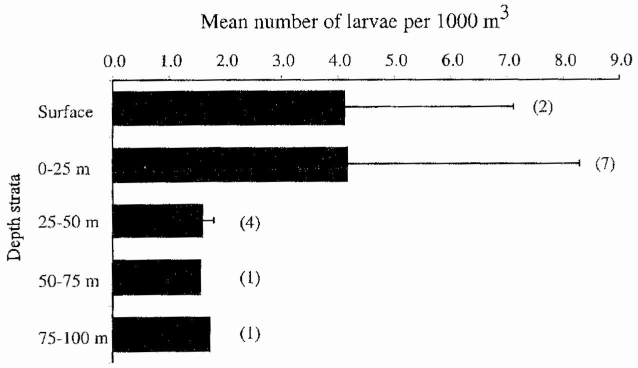


Fig. 4. Vertical distribution of *S. brama* larvae in Bass Strait (all records combined). Bars denote 1 s.d. Number in parentheses, number of tows that collected *S. brama* larvae within the specified depth stratum.

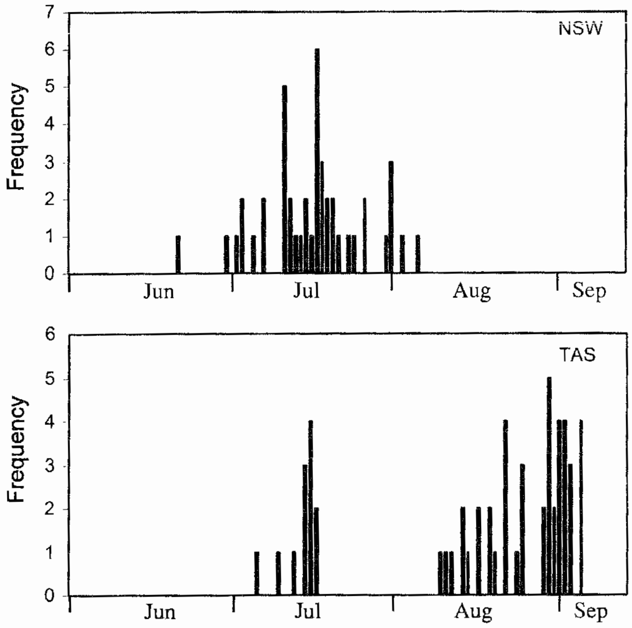


Fig. 5. Back-calculated spawning dates for *S. brama* larvae in southern Australia.

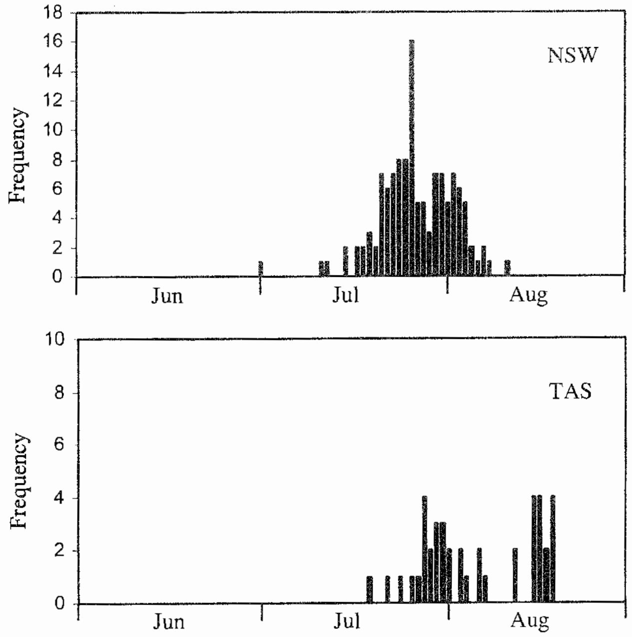


Fig. 6. Back-calculated spawning dates for *S. punctata* larvae in southern Australia.

Discussion

These data for larvae of both *Seriolella* species support previous work indicating that peak spawning occurs in winter, and that it occurs across broad areas of south-eastern Australia (Smith 1989; Knuckey and Sivakumaran 2001). However, the data also suggest that there are major regional differences in the magnitude and timing of spawning. This was most pronounced for *S. brama*.

The distribution of small *S. brama* larvae (<5.0 mm BL) suggests that this species spawns over a large area from Kangaroo Island in South Australia to southern Tasmania, with a major spawning ground located on the central-west and north-west coasts of Tasmania. However, we have based these conclusions on the distribution and age of small larvae (<5.0 mm BL) that are up to 10–13 days post-spawning. Hence, advection of larvae during this initial period has undoubtedly increased the area we attribute to spawning activity. These conclusions are consistent with field observations of running ripe *S. brama* in these areas (Knuckey and Sivakumaran 2001). Eggs of a *Seriolella* species were also recorded during blue grenadier egg surveys off the central-west coast of Tasmania in 1994 and 1995, further suggesting that this region is a spawning area (M. Lewis and C. Bulman, CSIRO Marine Research, personal communication).

The location of large concentrations of small *S. brama* larvae off eastern Vic./southern NSW combined with their almost complete absence between this area and southern Tasmania (including Bass Strait), suggests that separate major spawnings occur in this area. Similarly, differences in the timing of spawning between eastern Vic./southern NSW and western Tasmania also suggest separate spawning events. The timing of spawning from back-calculated age data was consistent with that derived from GSI data by Knuckey and Sivakumaran (2001) who also reported that *S. brama* east of Bass Strait spawned approximately one month earlier than those west of Bass Strait.

Very little information is available on spawning in *S. punctata*. Our data suggest a similar spawning period to that of *S. brama* in south-eastern Australia. The absence of *S. punctata* larvae in Victorian waters west of Bass Strait and in South Australia suggests that this species may not spawn in these areas. However, our sample coverage in these areas was poor, relative to other areas. *Seriolella punctata* appears to spawn between western Tasmania and southern NSW. Although there were peaks in the concentrations of larvae off both southern Tasmania and off southern NSW, small to moderate numbers of small *S. punctata* larvae were consistently captured between these two regions, suggesting that spawning by *S. punctata* is more continuous across this range. There was also considerably more overlap in back-calculated spawning dates for *S. punctata* between Tasmania and NSW, although there was a tendency for later spawning in more southerly locations.

There were very few vertically stratified samples taken in which *Seriolella* larvae were recorded, and thus our knowledge of their vertical distribution is limited. This limits the ability to adequately assess transport processes of larvae and the connectivity of regions through larval supply.

The ecology of small juveniles of each species is poorly documented, apart from observations of associations with scyphomedusae by Last *et al.* (1983). Juveniles are widespread in southern Australia and are often targeted by recreational fishers in bays and estuaries (Kailola *et al.* 1993), although no larvae or juveniles have been reported from Port Phillip Bay, Vic. (Neira, unpublished). Last *et al.* (1983) and Lyle and Ford (1993) reported that bays and estuaries of south-eastern Tasmania were major nursery areas for both species. The winter transport of larvae from spawning grounds off western Tasmania to nursery areas in coastal bays of south-eastern Tasmania by the Zeehan Current is well documented in blue grenadier (Gunn *et al.* 1989; Lyne and Thresher 1995). A similar transport of *Seriollela* larvae spawned in winter off the west coast of Tasmania is likely to be responsible for supplying the reported nursery areas in the south-east of that area.

Commercial catches of both *Seriolella* species peak during the spawning period and fishers regularly report the capture of running-ripe specimens (Smith 1989; Tilzey 1998). This suggests that both species aggregate during this period and are thus more susceptible to capture. Seasonal catch-rate trends in some regions also support a migration probably associated with spawning. Knuckey and Sivakumaran (2001) reported a marked decline in catch rates of *S. brama* off south-eastern Tasmania during winter, and suggested that this may indicate a north–south migration. An alternative explanation is that these fish migrate to primary spawning grounds off the west coast of Tasmania during this period.

In summary, the distribution and occurrence of larvae, as well as larval otolith data, support a winter or winter–spring spawning period for both *S. brama* and *S. punctata* in south-eastern Australia. Although spawning is widespread in both species, our data suggest that there are separate spawning grounds off the west coast of Tasmania and north-eastern Vic./southern NSW for *S. brama*. Spawning in *S. punctata* appears to occur in a more continuous region between south-western Tasmania and southern NSW. Whether *S. brama* is represented by separate eastern and western stocks in the SEF cannot be answered by these larval data alone and will depend on the extent of mixing in subadult and adult fish as well as spawning site fidelity. However, our data are not inconsistent with this hypothesis. The pattern for *S. punctata* is less clear, but our data suggest a more continuous link between populations in south-eastern Australia compared with that of *S. brama*.

Acknowledgments

This research was supported by grants from the Fisheries Research and Development Corporation (FRDC 92/019, 96/103 and 98/103). We thank I. Knuckey (MAFRI) for valuable discussions and T. Jones (CSIRO Marine Research) for assistance with database design.

References

Brothers, E. B., Mathews, C. P., and Lasker, R. (1976). Daily growth increments in otoliths from larval and adult fishes. *Fishery Bulletin (US)* **74**, 1–8.

Bruce, B. D., Sutton, C. A., and Thresher, R. E. (1996). An ichthyoplankton based analysis of the spawning distribution and stock structure of temperate Australian finfish. Final Report to FRDC #92/019. 65 pp.

Bruce, B. D., Sutton, C. A., and Neira, F. J. (1998). Centrolophidae – warehous. In 'The Larvae of Temperate Australian Fishes: a Laboratory Guide for Larval Fish Identification'. (Eds F. J. Neira, A. G. Miskiewicz and T. Trnski.) pp. 422–7. (University of Western Australia Press: Nedlands.)

Bruce, B. D., Young, J. W., Evans, K., Sutton, C. A., and Furlani, D. M. (In press). The influence of mesoscale physical oceanographic processes on larval distribution and stock structure in jackass morwong (*Nemadactylus macropterus*). *ICES Journal of Marine Science*.

Gavrilov, G. M., and Markina, N. P. (1979). The feeding ecology of fishes of the genus *Seriolella* (fam: Nomidae) on the New Zealand Plateau. *Journal of Ichthyology* **19**, 128–35.

Gomon, G. M., Glover, J. C. M., and Kuiter, R. H. (1994). 'The Fishes of Australia's South Coast.' (State Printer: Adelaide.) 992 pp.

Grimes, P. J., and Robertson, D. A. (1981). Egg and larval development of the silver warehou, *Seriolella punctata* (Pisces : Centrolophidae). *New Zealand Journal of Marine and Freshwater Research* **15**, 261–6.

Gunn, J. S., Bruce, B. D., Furlani, D. M., Thresher, R. E., and Blaber, S. J. M. (1989). Timing and location of spawning of blue grenadier, *Macruronus novaezelandiae* (Teleostei : Merlucciidae), in Australian coastal waters. *Australian Journal of Marine and Freshwater Research* **40**, 97–112.

Jenkins, G. P. (1987). Age and growth of co-occurring larvae of two flounder species, *Rhombosolea tapirina* and *Ammotretis rostratus*. *Marine Biology* **95**,157–66.

Kailola, P. J., Williams, M. J., Stewart, P. C., Reichelt, R. E., McNee, A., and Grieve, C. (1993). 'Australian Fisheries Resources.' (Bureau of Rural Resources and Fisheries Research and Development Corporation: Canberra.)

Knuckey, I. A., and Sivakumaran, K. P. (2001). Reproductive characteristics and per-recruit analyses of blue warehou (*Seriolella brama*): implications for the South East Fishery of Australia. *Marine and Freshwater Research* **52**, 575–87.

Last, P. R., Scott, E. O. G., and Talbot, F. H. (1983). 'Fishes of Tasmania.' (Tasmanian Fisheries Development Authority: Hobart, Australia.) 563 pp.

Lyle, J. M., and Ford, W. B. (1993). Review of trawl research 1979–1987, with summaries of biological information for the major species. Department of Sea Fisheries Tasmania Technical Report No. **46**, 169 pp.

Lyne, V. D., and Thresher, R. E. (1995). Dispersal and advection of *Macruronus novaezelandiae* larvae off Tasmania: simulation of the effects of physical forcing on larval distribution. In 'Multidisciplinary Studies of Recruitment of Australian Marine Populations'. (Ed. P. Sammarco.) (Springer: Berlin.)

MacDonald, C. M., and Smith, D. C. (1996). Blue warehou 1995, stock assessment report. South East Fishery Assessement Group. (Australian Fisheries Management Authority: Canberra.)

Neira, F. J., Miskiewicz, A. G., and Trnski, T. (1998). 'The Larvae of Temperate Australian Fishes: a Laboratory Guide for Larval Fish Identification.' (University of Western Australia Press: Nedlands.)

Smith, D. C. (1989). Summary of data available on the warehou *Seriolella brama* and *S. punctata*. Marine Science Laboratory Internal Report No.183. 26 pp. (Queenscliff: Australia.)

Smith, D. C. (1995). Blue warehou 1994, stock assessment report, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Thresher, R. E., Bruce, B. D., Furlani, D. M., and Gunn J. S. (1988). Distribution, advection and growth of larvae of the southern temperate gadoid *Macruronus novaezelandiae* in Australian coastal waters. *Fishery Bulletin US* **87**, 29–48.

Tilzey, R. D. J. (1998). Fishery assessment report. The South East Fishery 1998. (Bureau of Rural Sciences: Canberra.)

Young, J. W., Bradford, R. W., Lamb, T. D., and Lyne, V. D. (1996). Biomass of zooplankton and micronekton in the southern bluefin tuna fishing grounds off eastern Tasmania, Australia. *Marine Ecology Progress Series* **138**, 1–14.

Manuscript received 3 November 1999; revised and accepted 2 June 2000

Mar. Freshwater Res., 2001, **52**, 637–49

Age, growth and mortality of redfish *Centroberyx affinis*

A. K. Morison[A] *and K. R. Rowling*[B]

[A]Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Vic. 3225, Australia
[B]Cronulla Fisheries Centre, New South Wales Fisheries, PO Box 21, Cronulla, NSW 2230, Australia

Abstract. Age and growth of 5678 redfish, collected during 1991–98 from Australia's South East Fishery, were estimated from thin sections of otoliths. A maximum age of 44 years was recorded for a 30 cm (fork length) female, but 80% of females in the commercial catch were <10 years, and 80% of males were <13 years. The largest was a 34 cm female estimated to be 36 years old. Repeated age estimates of a subsample revealed an average error of 3.79%. There was significant variation in the mean length-at-age among years, and there were significant effects for age*year, age*sex, age*region, region*year, and sex*region*year interactions. Assessments of the fishery have assumed a single stock, because tagging results from the 1980s indicate movement of redfish along the coast. This study found consistent differences in sex ratio and growth rate between regions, which indicate some structuring within the population. However, the differences in growth rates are not consistent among years and could not be explained by differences in depths fished, suggesting a more dynamic situation than spatially segregated stocks. Estimates of natural mortality ranged from 0.07 to 0.11 year^{-1} and differed between regions.

Introduction

Redfish, *Centroberyx affinis*, are found in New Zealand and along Australia's south-eastern coast from southern Queensland to eastern Tasmania including Bass Strait (Kailola *et al.* 1993). They are one of 12 teleosts caught in Australia's South East Fishery (SEF), which are managed by an annually determined Total Allowable Catch. The main fishery for redfish is off the New South Wales (NSW) coast (Fig. 1) and the majority of the catch is taken in trawls at depths of 100–200 m (Rowling 1994).

Tagging studies suggest that there is a single stock off the NSW coast, although the genetic relationship with fish from other areas is unknown (Rowling 1994). Juveniles inhabit shallower inshore waters and adults are more abundant in

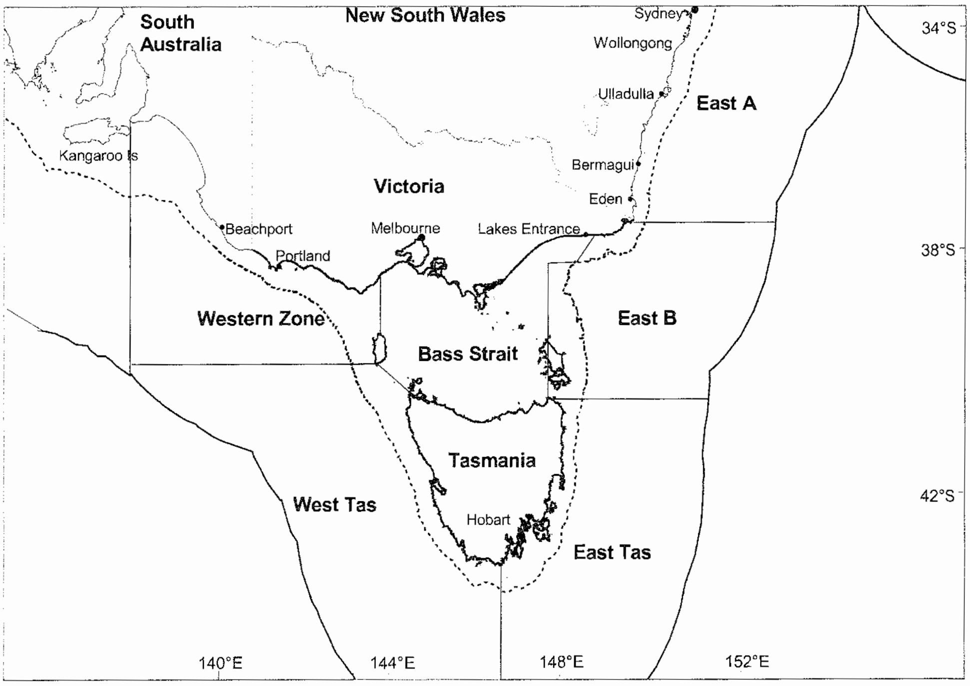


Fig. 1. Map of SEF showing fishing zones and major ports. The redfish fishery operates mainly in East A.

10.1071/MF00016 1323-1650/01/040637

deeper waters and are found to depths of 450 m (Kailola *et al.* 1993). Redfish caught in research trawls from inshore waters were found to be smaller than those caught from mid-shelf and offshore locations (Andrew *et al.* 1997). This distribution pattern suggests that there is an offshore movement of fish that is related to fish length (Chen *et al.* 1997).

The age and growth of redfish have been estimated by counting increments on whole otoliths (Diplock 1984). However, the results of tagging studies suggested that growth was slower than these age estimates indicated (Rowling 1990). Age estimates from sectioned otoliths yielded estimates of growth that were more consistent with the results from tagging studies (Smith and Robertson 1992; Smith *et al.* 1993), and the bomb-radiocarbon chronometer has since shown such age estimates to be the more accurate (Kalish 1995). Age estimates from sectioned otoliths have also been in agreement with known times of liberty (of up to 10 years) of tagged redfish (Morison, unpublished). Mortality estimates have been made based on the results of tagging work (Rowling 1990; Rowling 1994) and as part of a cohort analysis of the fishery (Tilzey 1999).

This paper presents the first formally published account of the age composition, growth and mortality of redfish based on age estimates made from sectioned otoliths. It examines in detail evidence from preliminary analyses for faster growth of redfish from more southern areas (Tilzey 1998; Rowling 1999). Stock structure is one of the main uncertainties in recent assessments of the fishery (Tilzey 1999), and evidence is examined for structuring within the redfish population from regional variation in sex ratios, growth and from the results of earlier tagging studies. This study also provides more reliable estimates of the length–age relationship for redfish, which Chen *et al.* (1997) suggested were needed for evaluating the yield-per-recruit analysis.

Methods

Otoliths were sampled from 5678 redfish from the commercial catches landed at ports on the New South Wales (NSW) and Victorian coasts. Samples were also obtained from the catch by research trawls conducted as part of trawl surveys of fish populations (Andrew *et al.* 1997). The sex and fork length (FL) rounded down to the nearest whole cm were provided with each otolith sample. The depth and exact location fished by the commercial vessels were often not known. However, data on the distribution by depth of shots containing redfish were obtained for each fishing year from the records provided by all licensed fishers to the Australian Fisheries Management Authority as a requirement of their fishing licence. These data were summarised for 50 m depth ranges and grouped into three regions by latitude: north of 34°S (Sydney/Wollongong), 34–45°S (Ulladulla), and south of 35°S (Eden/Bermagui).

Thin sections were prepared after embedding the otoliths in polyester resin following the method of Anderson *et al.* (1992). The otolith sections were illuminated with transmitted light at 15–25 × magnification and displayed on a black and white computer monitor by using a customized image analysis system (Morison *et al.* 1998). Opaque increments were counted on the proximal side of the otoliths on either the dorsal or ventral side of the sulcus acousticus, wherever the increments were clearest. More detail of the method is provided in Smith and Robertson (1992). Ages estimated by this method have been shown to provide accurate estimates of the true age of redfish by the application of the bomb-radiocarbon chronometer (Kalish 1995). Batches of otoliths for which data are reported are listed in Table 1.

Repeat readings of a subsample of 251 otoliths were used to estimate the index of average percent error (IAPE), a measure of the precision of the age estimates (Beamish and Fournier 1981). The IAPE is calculated as:

$$[\mathrm{IAPE}] = \frac{100}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{N}\frac{\left|X_{ij} - X_{j}\right|}{N}\right]$$

where N is the number of fish aged in the subsample, R is the number of times fish are aged, X_{ij} is the ith determination for the jth fish, and X_j is the average estimated age of the jth fish.

A linear regression of the second versus the first reading was used to test for significant bias between repeat readings and the confidence intervals for the slope and intercept were used to estimate a significant difference from unity or zero, respectively.

The von Bertalanffy growth function was fitted to the length and age data for samples by using the NLIN procedure in SAS, a non-linear, least squares procedure. From a grid search over a range of possible values for L_∞, K and t_0, the combination with the lowest residual sum of squares was selected as the starting point for iterations. Both the Secant and Marquardt iterative techniques were tried from this point, and the solution with the lowest sum of squares selected. Immature fish were allocated alternatively to either the male or the female samples. Growth functions were fitted to data for each sex separately and for the sexes combined (including samples of males, females and immature fish). This assumes that the growth of immature male and female fish is not significantly different. Differences in the fitted curves between the sexes and areas were tested by using a likelihood ratio test (Kimura 1980),

$$\chi^2 = [-N\ln({\sigma_\Omega}^2/{\sigma_\omega}^2)]$$

where N is the total number of fish in samples compared, ${\sigma_\omega}^2$ and ${\sigma_\Omega}^2$ are the variances for the hypotheses H_ω, that all parameters are equal, and H_Ω, that all parameters are not equal, respectively.

As a means of giving equal weighting to all age groups, and avoiding differences in growth curves simply due to the age range of samples, the von Bertalanffy growth function was also calculated for female and male redfish by using the mean lengths-at-age as the input data, rather than the individual data points.

Subsequent analyses also examined whether apparent differences in fish growth were attributable to gear selectivity, as some samples had been collected by the New South Wales research vessel RV *Kapala* by using a trawl net with a mesh size smaller than that used by commercial vessels (90 mm).

The generalized linear model procedure (Proc GLM) in SAS was also used to test for differences between sexes, areas and years in the mean length-at-age (with age as a covariate). Age was expressed as a real number with the decimal portion representing the proportion of the year from 1 January to the date of capture. For this analysis the dataset was reduced to known male and female fish, ages 3–16 years, areas Eden and Ulladulla, and years 1992, 1993, 1996 and 1997 so that there was a sample size of at least five fish from each of the combinations of variables. This reduced dataset included 3024 fish (53% of total sample) of 11–34 cm FL.

The Chapman–Robson estimator (Chapman and Robson 1960) was used to estimate total mortality. This estimator simplifies for large sample sizes to:

$$\hat{Z} = \ln\left[\frac{1 + \bar{A} - Tc}{\bar{A} - Tc}\right]$$

Table 1. Number of fish aged by year and sex for each area of the fishery

North includes fish landed in Sydney and Wollongong; Ulladulla includes fish landed in Ulladulla and Bateman's Bay; Eden includes fish landed in Eden, Bermagui and Tathra

Area	Year	Sex				Sex ratio	Total
		Female	Immature	Male	Unknown	F/M	
North	1991	121	0	119	3	1.02	243
	1994	0	157	0	0		157
	1997	0	0	0	10		10
	1998	25	0	26	0	0.96	51
	Sub-total	*146*	*157*	*145*	*13*	*1.01*	*461*
Ulladulla	1992	237	0	195	2	1.22	434
	1993	94	0	75	0	1.25	169
	1994	1	303	2	15	0.50	321
	1996	106	0	54	505	1.96	665
	1997	361	4	218	14	1.66	597
	1998	379	0	203	3	1.87	585
	Sub-total	*1178*	*307*	*747*	*539*	*1.58*	*2771*
Eden	1992	82	0	93	2	0.88	177
	1993	478	0	159	83	3.01	720
	1994	65	55	27	7	2.41	154
	1995	212	0	39	28	5.44	279
	1996	61	0	11	352	5.54	424
	1997	315	0	154	7	2.04	476
	1998	41	0	20	10	2.05	71
	Sub-total	*1254*	*55*	*503*	*489*	*2.49*	*2301*
Lakes Entrance	1994	85	0	12	1	7.08	98
	1997	31	0	16	0	1.94	47
	Sub-total	*116*	*0*	*28*	*1*	*4.14*	*145*
Grand Total		**2694**	**519**	**1423**	**1042**	**1.89**	**5678**

where $\hat{Z}$ is the total mortality, $\bar{A}$ is the mean age, and T_c is the age at full recruitment.

Natural mortality was estimated by using the 1% rule (Sparre and Venema 1992):

$$\hat{M} = \ln(100)/A_{\max}$$

where $\hat{M}$ is the natural mortality, and $A_{\max}$ is the maximum observed age.

Natural mortality was also estimated by using this equation but substituting the estimated age at 95% of L_∞ for the maximum observed age (Gulland 1983).

Results

Precision of age estimates

Repeated age estimates agreed with the original estimate in 51% of cases and 96% were within 2 years of the original estimate (Table 2). The distribution of the differences between the age estimates did not indicate any consistent bias between the two readings, although there are greater deviations between the two readings for older fish. The IAPE was 3.79%. An IAPE of less than 5% is indicative of

Table 2. Difference between repeat age estimates of redfish (1st–2nd Age), by 1st age estimate

1st–2nd Age	1st Age																											
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	26	28	29	31	35	All
–5																						1	1					2
–4																1						1						2
–3										1							2							1				4
–2				2	2	1	3								2					2					1			13
–1	1	3	10	7	9	2	2	1	1	3	1	1	1	2	1	1	1	1	1	1				1				51
0		3	21	27	21	11	5	7	6	5	3	1	1		3	2		2		3	4	1				1	1	128
1				3	7	3	6	3	1		2	1	1	1	1	1	1	1			1							33
2						2		1	1		3	1				3			1	1	1	1				2		17
3																							1					1
All	1	6	31	39	39	19	16	12	9	9	9	4	3	3	7	8	4	4	2	7	6	4	2	2	1	3	1	251

consistent interpretation of ages (Morison *et al.* 1998). From the regression of 2nd versus 1st readings, the 95% confidence intervals for the slope and intercept indicated that they were not significantly different from unity or zero, respectively, indicating no consistent trend in the differences between the two readings.

Size and age composition and sex ratios

The maximum estimated age for females was 44 years for a 30 cm FL fish collected in 1993. The largest females aged were two 34 cm FL fish both estimated to be 36 years old. The maximum estimated age for males was 37 years for a 28 cm FL fish collected in 1993. The largest male aged was a 33 cm FL fish estimated to be 31 years old.

Length–frequency distributions of the samples aged were usually unimodal with the mode at 20–22 cm FL (Fig. 2). The samples collected in 1994 were unusual in that they included more small fish from research samples collected by the RV *Kapala* and also a larger proportion of fish over 25 cm FL than in other years. In all but three years the length–frequency distributions of both females and males have similar modes and shapes. In 1994 the mean and mode for females was higher than for males. In 1995 and 1998 the mean lengths of females and males were similar, but the distributions for females showed no clear mode. Onboard observations have shown that all redfish less than 15 cm FL are discarded, those less than 20 cm FL are mostly discarded, those between 20 and 23 cm FL are mostly retained, and those over 23 cm FL are all retained (Liggins 1996). These discarding practices have been largely driven by industry-wide factors and are not known to vary from port to port. Prior to 1995, most samples from the commercial fishery were obtained from the retained portion of the catch (over 16 cm FL). Batches of otoliths obtained since 1995 have varied greatly in the size range of fish sampled but have included representative samples from both the retained and discarded portions of the catches.

When the length and age composition of samples was viewed as cumulative percent frequency distributions across all years (Fig. 3), there was a small difference between the sexes by length that translated to a larger but opposite difference by age. For example, 80% of females are less than about 23.5 cm FL, but the same percentile for males is about 1 cm smaller. However, 80% of females are less than 10 years of age, and the same percentile for males is about three years older. There are thus more older males than females but these tend to be smaller fish. These differences indicate different growth rates for females and males and also suggest that total mortality varies by sex.

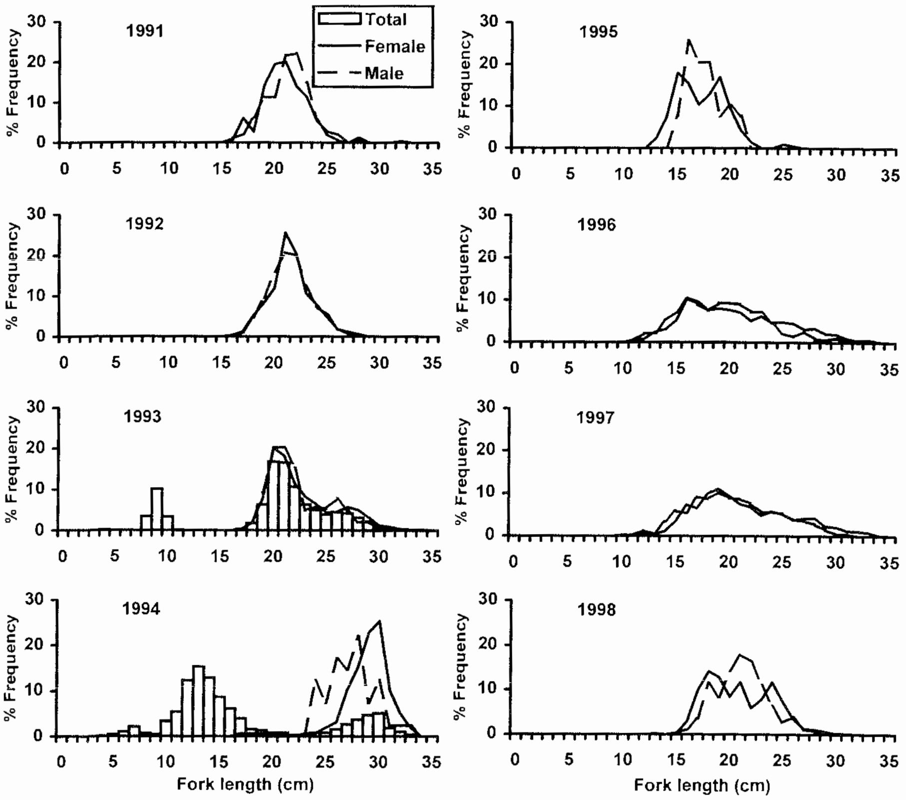


Fig. 2. Length–frequency distributions for aged samples of redfish for females and males, 1991–98, and for all sexes combined (total) in 1993 and 1994. Distributions combine samples from the retained and discarded portions of the commercial catch and from research trawls.

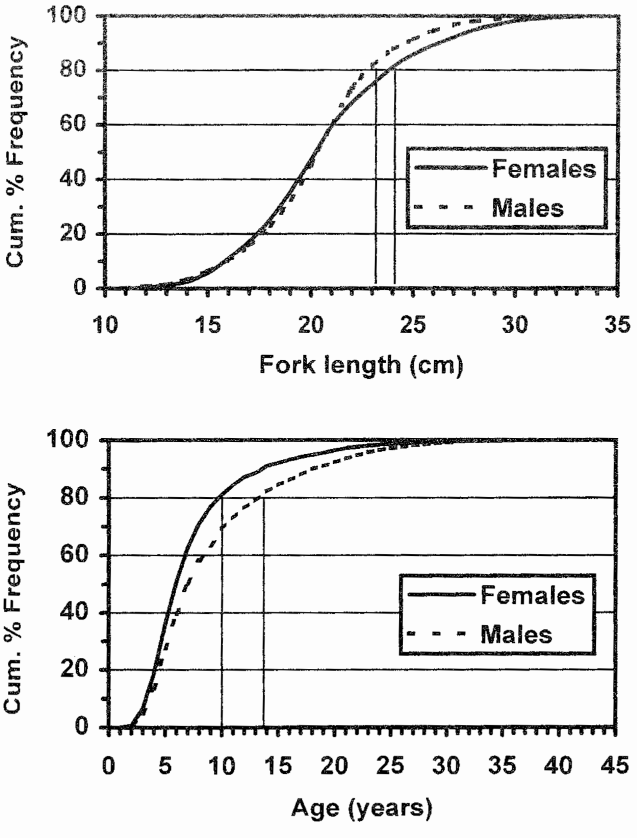


Fig. 3. Cumulative percent frequency distributions of redfish by sex for length (top) and for age (bottom); areas and years combined. Vertical lines mark the 80 percentiles for length and age of females and males.

The age composition of the aged sample is usually unimodal with the main mode (the age at full recruitment) at 5–8 years of age (Fig. 4). However, the age at full recruitment was as young as 3 years in 1994 and 1995 and as high as 10 years in 1991, with a greater proportion of fish under 5 years of age in the samples between 1994 and 1997. This is in accord with the higher proportion of fish less than 15 cm FL in these samples, which include fish normally discarded. In all years the majority of fish sampled were under 15 years of age. The differences in age composition among years are the same for females and males (Fig. 4). The age composition of the commercial catch suggests that the age at full recruitment to the fishery is 3–5 years.

The size composition of samples from Eden and Ulladulla shows a greater proportion of females less than 20 cm FL and males less than 18 cm FL in samples from the Ulladulla area and fewer fish over 25 cm FL (Fig. 5). However, the age composition of samples from these areas is very similar (Fig. 6).

Data on sex ratios within regions show a trend for an increasing proportion of females in samples from north to south (Table 1). In samples for which at least 100 fish were sexed, sex ratios at Ulladulla ranged from 1.22 to 1.96 and averaged 1.58; sex ratios at Eden were >2.0 in all years except 1992, reached 5.44 in 1995, and averaged 2.49.

Growth

The parameters of the von Bertalanffy growth function fitted to data for males and females (Table 3) showed significant differences between the sexes ($\chi^2 = 361$, df = 3, $P < 0.001$) for all regions combined. The comparison of the growth curves fitted to data from the Ulladulla and Eden regions was also significant for both females ($\chi^2 = 486$, df 3, $P < 0.001$) and males ($\chi^2 = 221$, df 3, $P < 0.001$). This difference between the sexes persisted when the function was fitted to the raw data and to the mean lengths-at-age. However, the von Bertalanffy growth functions fitted to mean length-at-age data produced a higher L_∞, lower K and smaller t_0 than for the raw data for both females and males. The growth curves fitted to the raw data did not describe the growth of older redfish as well as the curve fitted to the mean lengths-at-age. The observed lengths-at-age tended to lie below the line fitted to the raw data, as the curve fitting process gave greater weighting to the majority of observations for the younger age classes. Using the mean lengths gave equal weighting to all age classes and the fitted curve therefore passed closer to the observed mean lengths of all age classes.

Inspection of mean length-at-age data by year indicated that samples for 1994 from Eden had substantially higher mean lengths-at-age than other years (Fig. 7). This difference was evident in the age–length keys and was apparent for both females and males. To check whether this was due to errors in age estimation, 195 fish from this year, including the larger fish, were re-aged without reference to the previous estimates. These second readings agreed closely with the first (APE=4.9% and slope and intercept regression coefficients were not significantly different from unity and zero, respectively) and using the second readings in the analyses did not reduce the difference in mean length-at-age from the other years.

Plots of mean length-at-age showed the differences between the sexes that were identified in the fitted growth curves, but also indicated that there were larger differences between Eden and Ulladulla than between the two sexes (Fig. 8). Fish from the southern area showed a faster growth rate for fish 4 years and older. This difference between areas was consistent for both males and females (Fig. 9). However, the differences between sexes were smaller than those observed among years, particularly for the southern area (Fig. 7).

The generalized linear model was used to analyse the significance of the contributions of year, sex and area to the observed variation in mean length-at-age. This analysis of length-at-age showed a significant overall model effect (F = 129.56, $P < 0.0001$, $R^2 = 0.57$) (Table 4). There were no overall significant differences between the areas but there

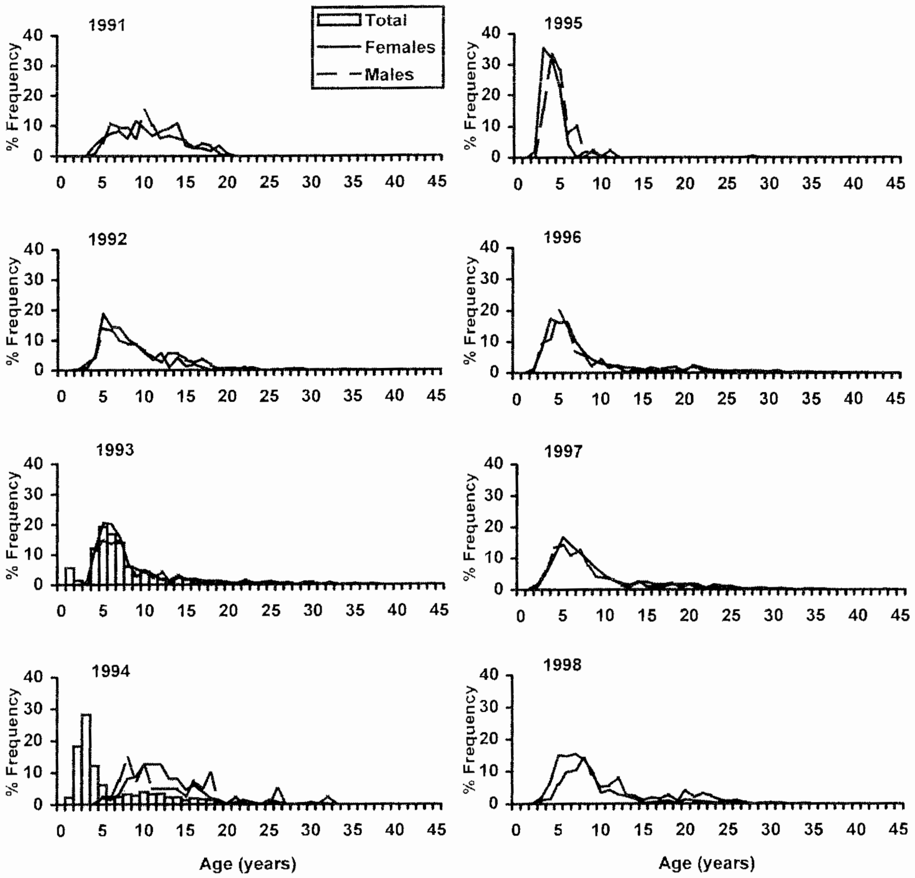


Fig. 4. Age composition of the aged samples of female and male redfish, 1991–98, and for all sexes combined (total includes immature fish and those of unknown sex) in 1993 and 1994.

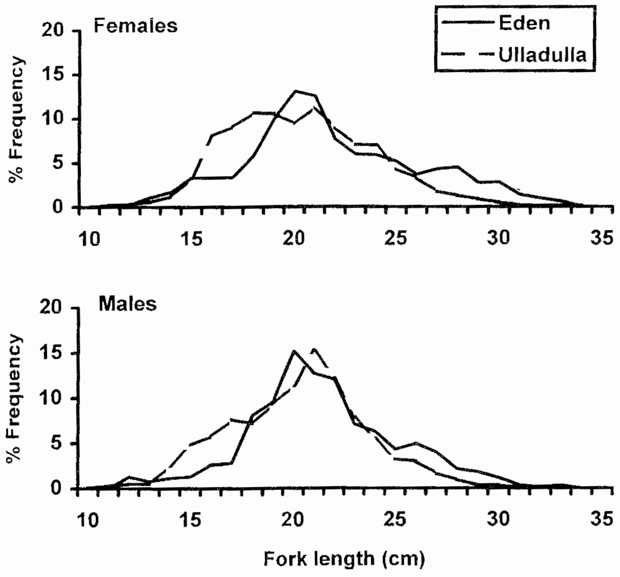


Fig. 5. Length–frequency distribution of redfish by area for females (top) and males (bottom). Data for 1991–98 combined.

was a significant age*region interaction, reflecting the fact that the observed differences in growth between the regions are smaller for younger fish. Similarly, although there was no overall significant difference between the sexes, there was a significant sex*age interaction, as the differences in growth are only significant for older mature fish. There was a significant year effect indicating that there were significant differences among years in the length-at-age, and also a significant region*year interaction, indicating that the difference between the years was not the same for both regions. The testing of differences between the years included in the analysis showed that the redfish mean lengths-at-age for 1992 and 1993 were significantly different from each other and from 1996 and 1997, but that these latter two years were not significantly different from each other. Finally, there was also a significant three-way interaction for sex*region*year, indicating that the region*year interaction was different for males and females.

The relatively large differences in mean lengths-at-age between years were initially suspected to reflect either bias in length measurement or age estimation errors. These possibilities were also explored by comparing the

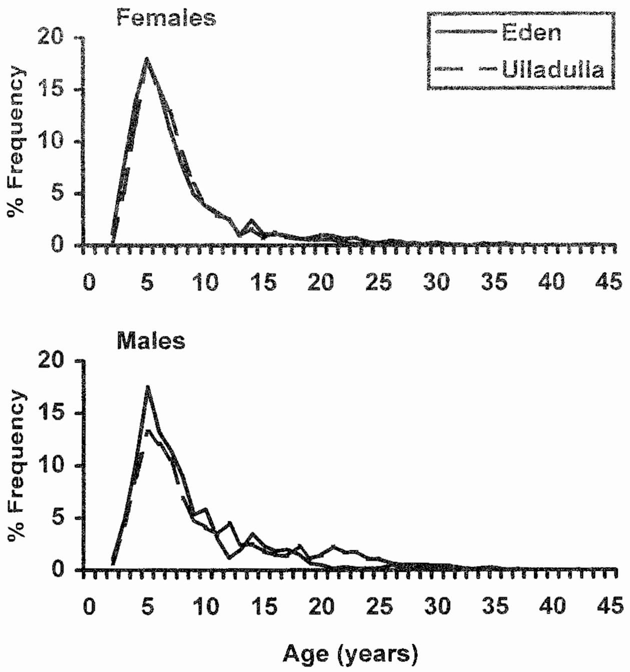


Fig. 6. Age composition of redfish by area for females (top) and males (bottom). Data for 1991–98 combined.

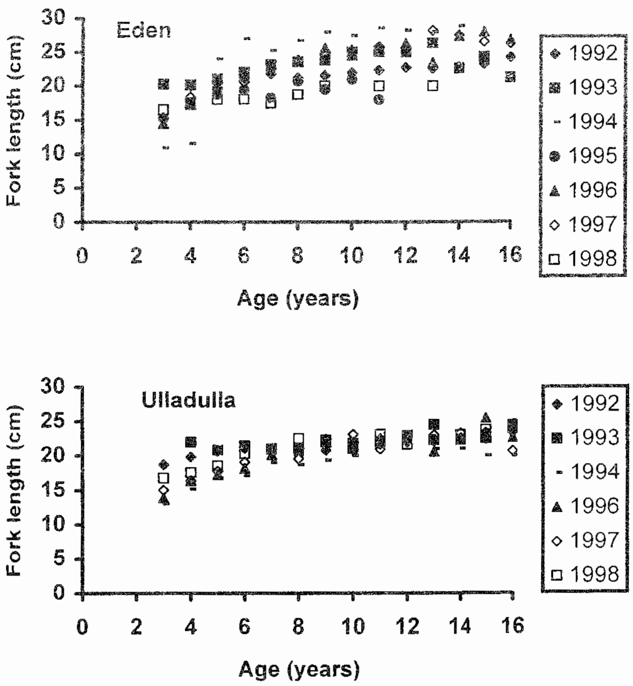


Fig. 7. Comparison of mean length-at-age among years (sexes combined) for samples collected from both Eden (top) and Ulladulla (bottom) areas. Fish aged 3–16 years only.

relationship between otolith weight and fish length for samples from the commercial catch with that from research samples. These otolith weight–fish length relationships would not be affected by age estimation errors and any errors in the length measurements would not appear in samples from both sources as data from the research vessel were collected by different technicians. There were obvious differences in the relationships between samples from the Eden and Ulladulla regions and similar differences were present in samples from both the commercial catch and the research samples (Fig. 10). This supports the validity of the finding that length-at-age

Table 3. Parameter estimates for the von Bertalanffy growth function for redfish

Estimates are based on mean lengths for each age (Mean *L*) and on lengths for individual fish (Raw data). Asymptotic standard errors (s.e.), and asymptotic 95% confidence intervals (95% C. I.) are for the latter parameter estimates

Region	Sex	*N*	Parameter	Estimate (Mean *L*)	Estimate (Raw data)	s.e.	95% C. I. Lower	95% C. I. Upper
All	Females	3455	L_∞	27.094	26.60	0.158	26.29	26.91
			K	0.203	0.224	0.006	0.211	0.237
			t_0	–0.810	–0.695	0.098	–0.887	–0.504
	Males	2021	L_∞	24.844	23.75	0.126	23.50	23.99
			K	0.198	0.280	0.008	0.263	0.297
			t_0	–1.193	–0.032	0.092	–0.497	–0.137
Ulladulla	Females	1591	L_∞	25.851	25.08	0.206	24.68	25.48
			K	0.178	0.218	0.010	0.200	0.237
			t_0	–1.410	–1.03	0.170	–1.37	–0.702
	Males	1095	L_∞	24.242	23.22	0.150	22.93	23.52
			K	0.189	0.259	0.011	0.238	0.281
			t_0	–1.449	–0.620	0.154	–0.921	–0.319
Eden	Females	1462	L_∞	27.899	28.20	0.267	27.68	28.72
			K	0.231	0.219	0.010	0.199	0.240
			t_0	–0.533	–0.676	0.167	–1.00	–0.350
	Males	625	L_∞	25.705	25.26	0.262	24.75	25.78
			K	0.238	0.290	0.018	0.254	0.326
			t_0	–0.651	–0.053	0.195	–0.435	0.330

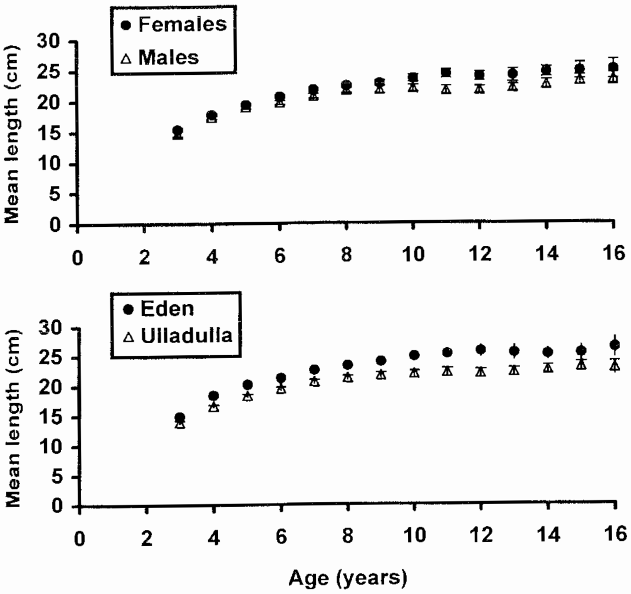


Fig. 8. Comparison of mean length-at-age (+/2 s.e.), between sexes (top) and areas (bottom), of aged redfish from South and Ulladulla regions, 1991–1998. Fish aged 3–16 years only.

varies between regions.

Distribution of trawl effort by depth

The depth distribution of trawl shots containing redfish was very similar for the two regions (Fig. 11), with most shots in the 150–250 m depth range. In these regions, shots were concentrated in shallower depths in the 1992–93 period. However, this apparent shift in fishing effort was most probably an artefact of a loophole in reporting requirements in these years that encouraged fishers to report catches as coming from shallower inshore areas. The similarity of depths fished in the Ulladulla and Eden areas means that the differences in mean length-at-age observed between these areas cannot be explained by the previously reported tendency for larger fish to inhabit deeper waters (Chen *et al.* 1997).

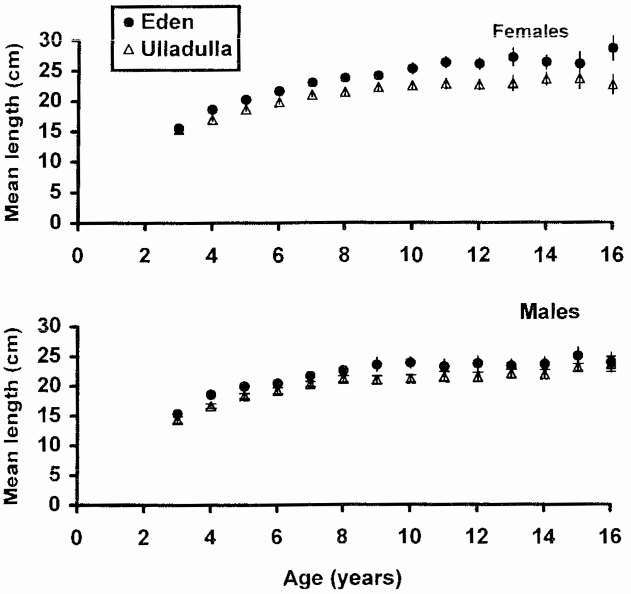


Fig. 9. Comparison of mean length-at-age (+/2 s.e.), between areas for females (top) and males (bottom), of redfish aged 3 and16 years, all years combined.

Movements of redfish from tagging studies

Significant latitudinal movements were observed for a small number of tagged redfish recaptured from a tagging study conducted in 1985–86 (Rowling 1990). Both northward and southward movements were recorded (Fig. 12); however, in the southern areas (from Bermagui south) only northerly movements were recorded, despite significant fishing effort in the area off Eden and further south. Despite the fact that only small numbers of fish were tagged in the southern areas during this study, the recapture rate for fish tagged in the Eden and Bermagui areas was about 1.8%, or six times the recapture rate reported for redfish tagged in the Wollongong/Ulladulla area (0.3%). No movements of tagged fish were recorded from the northern areas into the Eden area, although some movements were recorded from Eden to the adjacent northern areas.

Mortality estimates

The maximum estimated age of 44 years produces an estimate of natural mortality of 0.10 year^{-1} using the 1% rule. Using the same method but applying it to the age at 95% of L_∞ (40 years) gives an estimate of 0.12 year^{-1}.

Chapman and Robson estimates of total mortality, based on the average age beyond the age of full recruitment (set at 4 years) were 0.180 year^{-1} for a combined age composition, but were as high as 0.243 year^{-1} for Eden samples and as low as 0.152 year^{-1} for samples from Ulladulla (Table 5). These regional differences were not sensitive to changes to the age at full recruitment between 3 and 5 years. The differences between regions were consistent for both females and males, and the mortality estimates for females were higher than for males. Thus mortality estimates were highest for females from the Eden area (0.255 year^{-1}) and lowest for males from Ulladulla (0.132 year^{-1}).

Discussion

The age composition of redfish sampled between 1991 and 1998 shows that, despite being fished since 1915, and being subject to relatively heavy fishing pressure since the 1960s (Tilzey 1999), the population still contained small numbers of fish over 40 years of age, and that 8% of females and almost 16% of males in the aged samples were over 15 years of age. There has been a continual decline in the mean length of landed redfish since 1975 (Rowling 1993), which may have been influenced by the significant, but largely

Table 4. Results of GLM analysis of mean length-at-age by sex, area and year
Significant effects are shown in bold

Source	df	Type III SS	Mean Square	F Value	$P > F$
Age	**1**	**6417.677**	**6417.677**	**1233.89**	**0.0001**
Sex	1	0.0208	0.0208	0.00	0.9495
Year	**3**	**1629.432**	**543.144**	**104.43**	**0.0001**
Region	1	16.903	16.903	3.25	0.0715
Age*Sex	**1**	**59.232**	**59.232**	**11.39**	**0.0007**
Sex*Region	1	9.214	9.214	1.77	0.1833
Age*Region	**1**	**92.869**	**92.869**	**17.86**	**0.0001**
Age*Sex*Region	1	18.753	18.753	3.61	0.0577
Sex*Year	3	14.074	4.691	0.90	0.4393
Age*Year	**3**	**1475.894**	**491.965**	**94.59**	**0.0001**
Age*Sex*Year	3	20.279	6.760	1.30	0.2728
Region*Year	**3**	**53.216**	**17.739**	**3.41**	**0.0168**
Sex*Region*Year	**3**	**56.706**	**18.902**	**3.63**	**0.0124**
Age*Region*Year	3	21.786	7.262	1.40	0.2420
Age*Sex*Region*Year	3	28.527	9.508	1.83	0.1398

unrecorded, discarding of small fish through the history of the fishery.

The growth of redfish

The results of the present study confirm preliminary suggestions (Smith and Robertson 1992; Smith *et al.* 1993) that redfish grow more slowly and reach older ages than had previously been reported by Diplock (1984).

Additionally, it was found that there is more spatial and temporal variation in redfish growth than had been previously suspected. This variation in mean length-at-age of redfish occurs (*i*) from north to south, with faster growth in the south, but with the magnitude of the differences not consistent from year to year, (*ii*) from year-to-year, particularly in the south, and (*iii*) between the sexes, with females growing faster than males. The difference in growth between the sexes is common in teleosts, including those found in the SEF (Morison 1996) and reflects the differential allocation of energy into growth and gamete production between the sexes. Redfish mature at 4–6 years of age (Tilzey 1999). The variation between years and areas is harder to explain, because redfish are thought to comprise a single stock, based on tagging and other studies (Tilzey 1999). This variation may be attributable to any of at least six possible causes acting singly or in combination:

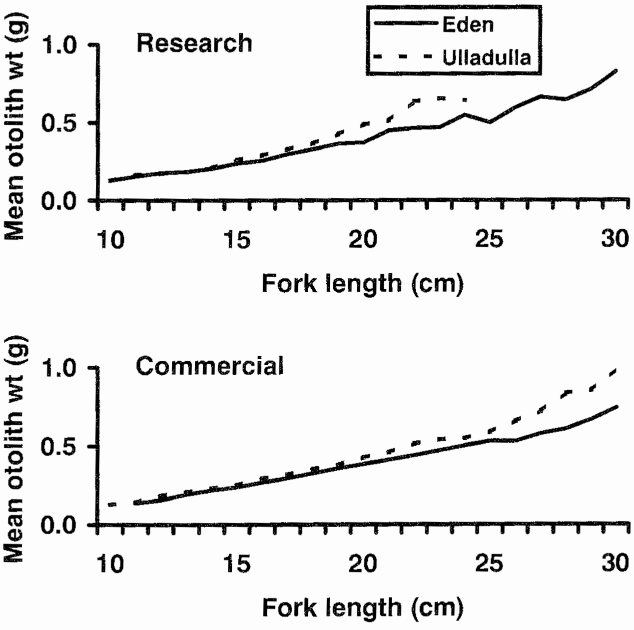


Fig. 10. Mean otholith weight by fish length for redfish from Eden and Ulladulla regions colected from research trawls (top) and comercial catches (bottom), 1991–1998.

(*1*) errors in age estimates;

(*2*) unrepresentative sampling of fish from the catch;

(*3*) gradual change in growth rates from north to south along the coast due to varying food availability, fish density, water temperature, or other environmental conditions, with no distinct stock boundaries;

(*4*) separate subpopulations (ecological stocks) with differences in growth over broad distances, with at least one distinct stock boundary between the Ulladulla and south areas;

(*5*) separate subpopulations between Eden and Ulladulla, and with differences in growth over small distances within the Eden area from which fish have been differentially sampled in different years;

(*6*) no separate subpopulations between Eden and Ulladulla but with movement of fish with different growth histories from outside the main fishing areas into and out of the Eden fishing area in some years.

The precision of the age estimates and the results of the

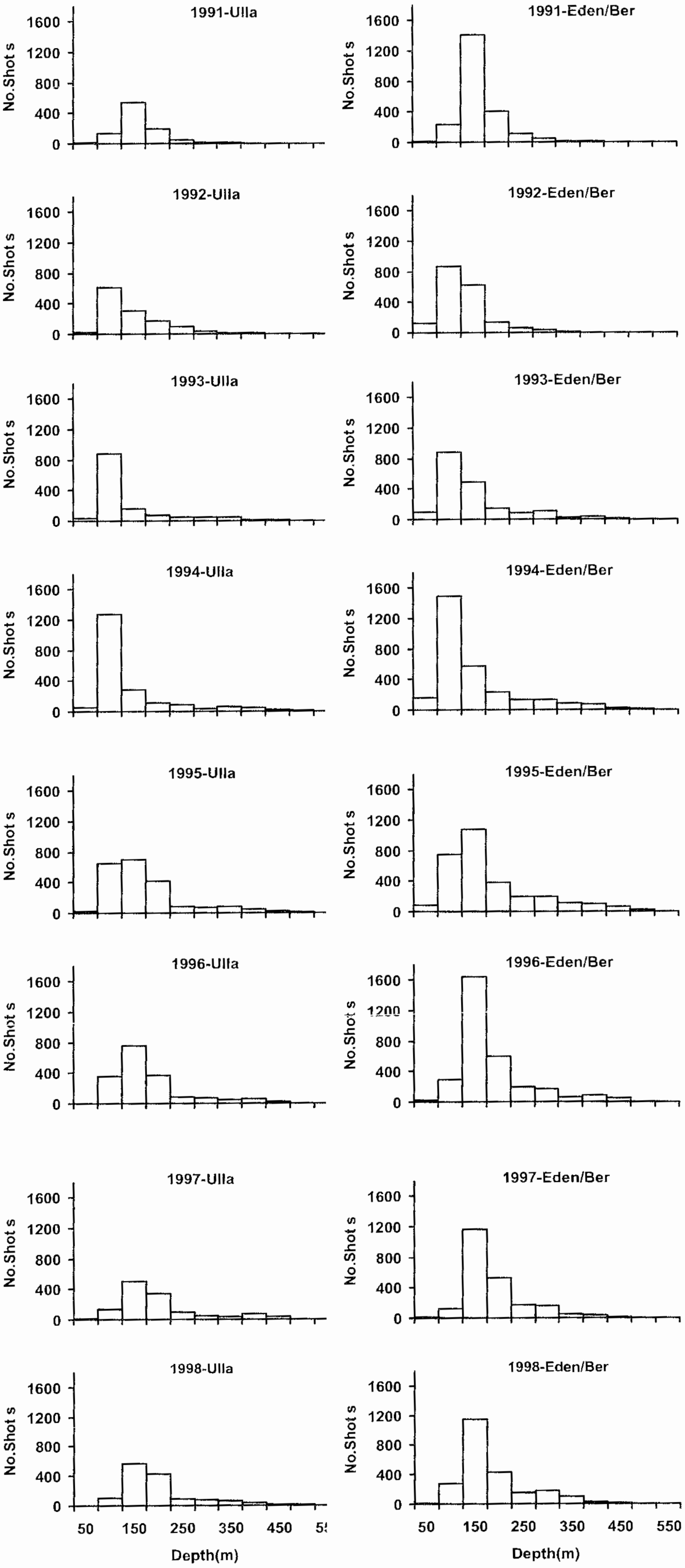


Fig. 11. Depth distribution of shots containing redfish, by latitude region: Ulla, Ulladulla; Eden/Ber, Eden and Bermagui.

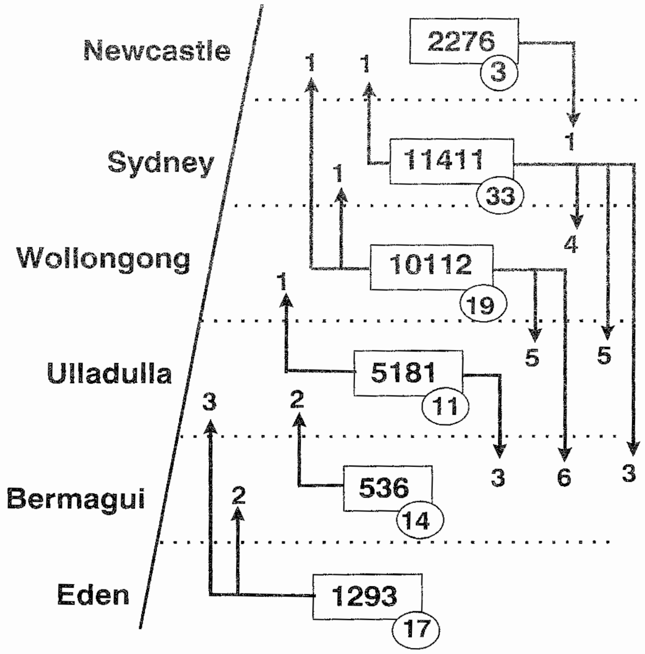


Fig. 12. Schematic diagram of regions along the NSW coast showing the numbers of redfish tagged within each region (within rectangles) and recaptured within the same region (within circles) or within other regions (arrowed).

repeated age estimates for the 1994 sample indicate that ageing errors did not contribute significantly to the observed variation in mean length-at-age. Errors in ageing are likely to be random, and would not be expected to produce the observed variation in growth between areas and years. The ageing method has also been well validated by the bomb radiocarbon chronometer (Kalish 1995).

The samples used in the analysis are believed to be representative of at least the retained portion of the commercial catch for most years sampled, because a comparison of the length–frequency distributions from on-board sampling shows no major bias (Liggins 1996). In any case, any length-selective bias in the sampling would not be expected to influence the mean length-at-age across such a range of ages or in so consistent a manner.

A gradual change in growth rates with latitude would be consistent with much of the observed variation. The few samples from the Sydney area (to the north of Ulladulla) show growth rates possibly slower than those from Ulladulla. Similarly the few samples from Lakes Entrance (to the south of the Eden area) show growth rates at least as fast as those from the Eden area. However, such a latitudinal trend would be expected to be relatively constant and therefore does not explain the observed year-to-year variation.

The possible existence of separate stocks, with a boundary between Ulladulla and Eden areas, would be unusual for a species that is so common and widespread along this section of coast. Such structuring is not known for other species caught in the SEF, although this has not been explored in detail and does not preclude it occurring for redfish. There are no known oceanographic boundaries in the area that could help establish and maintain a stock separation. There is a general north-to-south flow of the East Australia Current along this section of coast, but it has a complex eddy structure that is variable on a variety of time-scales, which makes it difficult to define the spatial structure

Table 5. Estimates of total mortality (*Z*) for redfish based on the Chapman and Robson equation

Mean age is mean of fish older than the age at full recruitment

Sex	Region	Variable	Age at Full Recruitment (years)		
			3	4	5
All	Ulladulla	Mean age	9.78	10.08	10.50
		Z	0.138	0.152	0.167
	Eden	Mean age	7.15	7.64	8.44
		Z	0.216	0.243	0.255
	All regions	Mean age	8.66	9.08	9.73
		Z	0.163	0.180	0.192
Female	Ulladulla	Mean age	8.94	9.21	9.65
		Z	0.156	0.175	0.195
	Eden	Mean age	7.06	7.44	8.22
		Z	0.220	0.255	0.271
	All regions	Mean age	8.30	8.63	9.29
		Z	0.173	0.195	0.210
Male	Ulladulla	Mean age	10.85	11.10	11.45
		Z	0.120	0.132	0.144
	Eden	Mean age	8.30	8.55	9.23
		Z	0.173	0.199	0.212
	All regions	Mean age	10.04	10.27	10.74
		Z	0.133	0.148	0.161

of the current (Chiswell *et al.* 1997). Knowledge of this current system is also on a broader spatial scale than is relevant for understanding the regional variation in redfish growth.

The consistency of the differences across a range of age classes indicates that this separation has been stable over a period of more than a decade and cannot be attributed to a local short-term variation in such factors as food availability. However, the differences observed among years in mean length-at-age in the Eden area in particular, suggest that there are short-term variations in mean length-at-age within this area that cannot be explained by changes in growth of resident fish. If fish within this area experienced conditions favouring more rapid growth even for only one year, these effects would still be apparent in subsequent years and the mean lengths-at-age would not return to lower levels in the following year.

An alternative explanation is that samples have been drawn from different subpopulations with different growth histories. This may occur if fishers were making catches from different areas in different years, but no spatial change in fishing areas is evident in the catch locations reported on daily fishing logbooks, or in records of reports by industry representatives at stock assessment meetings (Tilzey 1999). This pattern may also occur with no change to the distribution of fishing activity, if samples were not representative of the spatial or depth distribution of the catches in each year.

Movement of different subpopulations of redfish into the fishing areas would be expected to be reflected in changes in availability or catchability of redfish. Indeed changes in catchability of redfish have been raised in stock assessment meetings as a possible explanation of increased catches of redfish in the early 1990s (Rowling 1997). These observed changes were thought to be the result of increased recruitment as there were no indications of a greater representation of larger or older fish in the samples. However, the data presented here suggest an alternative explanation of subpopulations that can be differentiated on their growth rate, rather than their age or size composition. The increased catches of redfish were reported in 1993 and the higher growth rates were evident for some younger age classes in this year, but for most age classes not until 1994. Nevertheless, we believe that some structuring within the redfish stock is likely given the observed spatial and temporal variation in mean length-at-age and in sex ratios. The size composition of redfish catches measured at sea by observers from 1993 to 1998 from vessels off Eden are different from those from vessels off Ulladulla, being much more variable and showing no consistent trends (Rowling 1999). These observations are not subject to the sampling bias that may affect the aged sample, yet provide further evidence of differences in the characteristics of the redfish populations in the two areas.

Mortality estimates

Previous estimates of total mortality from tagging work were substantially higher than those suggested by the present analyses, being in the range 0.7–1.2 year^{-1}, with estimates of fishing mortality in the range 0.04–0.06 year^{-1} (Rowling 1990). There were a number of uncertainties with these earlier estimates including the mortality rate due to tagging, which, if it were underestimated, would have led to an overestimate of the total mortality. Such high mortality rates are inconsistent with the observed age composition of the redfish stock, and the maximum ages recorded for the species. The variation in age composition between the sexes and regions produced total mortality estimates that vary similarly. Future modelling of the redfish fishery may need to incorporate higher estimates of total mortality for females than males and higher estimates for the Eden area than for Ulladulla.

Conclusion

Differences in sex ratio, size composition and growth rates of redfish sampled from the Eden and Ulladulla areas indicate that there is significant structuring within what has previously been regarded as a single stock of redfish in the SEF. Results of earlier tagging work are also consistent with these observed differences. Year-to-year variation in the differences is consistent with previously suggested variation in catchability of redfish, especially for the Eden area. Estimates of total mortality are lower than suggested by earlier tagging work and are probably higher in the Eden area than further north, and higher for females than for males. A carefully designed sampling program over several years, stratified by area and depth, would be needed to more fully describe the spatial and temporal nature of the structuring within the redfish population.

Acknowledgments

Funding for the collection of otoliths and age estimation for redfish was provided by the Australian Fisheries Management Authority. Otolith collections were arranged or undertaken by Kevin Rowling, Geoff Liggins, Jeff Nemec, and David Makin of NSW Fisheries, and Ken Smith and Ian Knuckey of the Marine and Freshwater Resources Institute (MAFRI). Registration, weighing, sectioning and reading of otoliths were undertaken by Kylie Hall, Simon Robertson, Corey Green and Kyne Krusic-Golub of the Central Ageing Facility at MAFRI. Data on the depth distribution of shots was provided by Ian Knuckey. Data analysis was assisted by Ann Gason and Miriana Sporcic. Terry Walker assisted with estimation of mortality and David Smith is also thanked for his assistance with many phases of this work.

References

Anderson, J. R., Morison, A. K., and Ray, D. J. (1992). Validation of the use of thin sectioned otoliths for determining the age and growth of Golden Perch *Macquaria ambigua* (Perciformes : Percichthyidae) in the lower Murray Darling Basin, Australia. *Australian Journal of Marine and Freshwater Research* 43, 231-256.

Andrew, N. L., Graham, K. J., Hodgson, K. E., and Gordon, G. N. G. (1997). Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. New South Wales Fisheries Final Report Series No. 1 December 1997. (New South Wales Fisheries Research Institute: Sydney.)

Beamish, R. J., and Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Journal of the Fisheries Research Board of Canada* 36, 1395-1400.

Chapman, D. G., and Robson, D. S. (1960). The analysis of a catch curve. *Biometrics* 16, 354-368.

Chen, Y., Liggins, G. W., Graham, K. J., and Kennelly, S. J. (1997). Modelling the length-dependent offshore distribution of redfish, *Centroberyx affinis*. *Fisheries Research* 29, 39-54.

Chiswell, S. M., Toole, J., and Church, J. (1997). Transports across the Tasman Sea from WOCE repeat sections: the East Australian Current 1990-94. *New Zealand Journal of Marine and Freshwater Research* 31, 469-475.

Diplock, J. H. (1984). A synopsis of available data on redfish *Centroberyx affinis* from NSW waters. Working papers, Demersal and Pelagic Fisheries Research Group Workshop on Trawl Fish Resources 27-29 pp. March 1984. (New South Wales Fisheries Research Institute: Sydney.)

Gulland, J. A. (1983). Fish Stock Assessment: A Manual of Basic Methods. 223 pp. (John Wiley: Chichester.)

Kailola, P. J., Williams, M. J., Stewart, P. C., Reichelt, R. E., McNee, A., and Grieve, C. (1993). Australian Fisheries Resources. (Bureau of Resource Sciences: Canberra.)

Kalish, J. M. (1995). Application of the bomb radiocarbon chronometer to the validation of redfish *Centroberyx affinis* age. *Canadian Journal of Fisheries & Aquatic Sciences* 52(7), 1399-1405.

Kimura, D. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77, 765-766.

Liggins, G. (1996). The interaction between fish trawling (in New South Wales) and other commercial and recreational fisheries. Final Report, FRDC Project 91/79 (Fisheries Research Institute: Sydney.)

Morison, A. K. (1996). Age and Growth of Major Species in the South East Fishery. 18 pp. (Marine and Freshwater Resources: Queenscliff.)

Morison, A. K., Robertson, S. G., and Smith, D. C. (1998). An integrated system for production fish aging: image analysis and quality assurance. *North American Journal of Fisheries Management* 18, 587-98.

Rowling, K. R. (1990). Estimation of fishing mortality, stock unity and growth of redfish *Centroberyx affinis* by tagging. Final report of the redfish tagging study, New South Wales. Final Report of the Redfish Tagging Study, N.S.W. (FIRTA Project 85/71) (New South Wales Department of Agriculture and Fisheries, Fisheries Research Institute: Sydney.)

Rowling, K. R. (1993). Detailed assessment of redfish stocks urgently needed. *Australian Fisheries* 52(6), 20-22.

Rowling, K. R. (1994). Redfish, *Centroberyx affinis*. In 'The South East Fishery'. (Ed. Tilzey, R. D. J.) pp 149-158. (Bureau of Resource Sciences, Australian Government Print Service: Canberra.)

Rowling, K. R. (1997). Redfish Workshop. 21st - 22nd April 1997. Workshop report compiled for the South East Fishery Assessment Group 27 pp. (New South Wales Fisheries Research Institute: Sydney.)

Rowling, K. R. (1999). Redfish 1999 Stock Assessment Report. Redfish Assessment Group. South East Fishery Assessment Group (Australian Fisheries Management Authority: Canberra.)

Smith, D. C., Morison, A. K., and Robertson, S. G. (1993). How old are redfish, *Centroberyx affinis*? Prepared for Redfish Resource Assessment Workshop, BRS 14-16 April 1993. CAF Report. (Victorian Fisheries Research Institute, Department of Conservation and Natural Resources: Queenscliff, Victoria.)

Smith, D. C., and Robertson, S. G. (1992). Age determinations for redfish *Centroberyx affinis*, from samples submitted to the Central Ageing Facility: 1991/92. Internal Report No. 203 (Marine Science Laboratories: Queenscliff, Victoria.)

Sparre, P., and Venema, S. C. (1992). Introduction to tropical fish stock assessment. Part 1. Manual. FAO Fisheries Technical Paper No. 306/1 Rev. 1 376 pp. (FAO: Rome.)

Tilzey, R. D. J., editor. (1998). The South East Fishery 1997. Fishery Assessment Report compiled by the South East Fishery Assessment Group. 214 pp. (Australian Fisheries Management Authority: Canberra.)

Tilzey, R. D. J., editor. (1999). The South East Fishery 1998. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Manuscript received 9 February 2000; revised and accepted 9 October 2000

Mar. Freshwater Res., 2001, **52**, 651–60

Age, growth and spatial and interannual trends in age composition of jackass morwong, *Nemadactylus macropterus*, in Tasmania

Alan R. Jordan

Marine Research Laboratories, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Crayfish Point, Taroona, Tas. 7053, Australia

Abstract. Transverse sections of sagittae were examined. The first and second annual increments were defined by examination of the progression of otolith radius and length of the 0+ and 1+ cohorts. Growth in both sexes is rapid until ~5 years old (32–35 cm), and then slows appreciably. There was a broad range of lengths within individual age-classes, with a maximum of 12 age-classes present in a 1 cm length-class. Maximum ages of males and females were 41 and 30 years, respectively, which is considerably higher than previously estimated from whole otoliths. There was no significant difference in the growth curves between males and females, although this is influenced by the large number of juveniles and by the examination of relatively few large, older fish. The sex-specific von Bertalanffy growth parameters are: L_∞ 38.4 cm FL, t_0 –0.07 years, K 0.36 year^{-1} for females and L_∞ 36.2 cm FL, t_0 0.15 years, K 0.42 year^{-1} for males. The age composition was dominated by 4–7 year olds but showed evidence of considerable recruitment variability, particularly in the strong 1988 year-class. The relationship between the life-history strategy of *N. macropterus* and recruitment variability is discussed.

Introduction

Jackass morwong, *Nemadactylus macropterus*, is a common demersal species found throughout continental shelf waters of southern Australia and is an important species in the South East Fishery. Estimates of age and growth for *N. macropterus* revealed that growth is initially fast, with reported maximum ages of 11 years for males and 16 years for females from southern New South Wales/north-eastern Victoria (Smith 1982), and 11 years for males and 13 years for females from eastern Bass Strait (Wankowski *et al.* 1988). Both of these studies, however, were based on whole sagittal otoliths, with a recent reappraisal of ages from sectioned otoliths suggesting that maximum ages are considerably higher than previously estimated (Morison 1996). This is consistent with Vooren (1977) who reported a maximum age of 41 years for *N. macropterus* from New Zealand using a combination of whole, and broken and burnt sagittae. These general findings are also consistent with previous studies where ages were underestimated in whole otoliths compared with those sectioned or broken and burnt (Beamish 1979; Collins *et al.* 1988).

Estimates of population age-structure of *N. macropterus* in New Zealand waters indicate considerable recruitment variability, although such variations are not evident in all stocks (Vooren 1977). In south-eastern Australia, estimates of age compositions show little evidence of such variations (Wankowski *et al.* 1988); however, variations between years in the relative abundance of 25–30 cm fish led Smith (1989) to conclude that recruitment was variable. There is also recent evidence of recruitment variability in *N. macropterus*, with some indication of strong year-classes every 4–5 years (Tilzey 1999).

Given the lack of information on age and growth of *N. macropterus* from sectioned sagittal otoliths, the aims of this paper are to *(1)* determine the age and describe the growth of *N. macropterus* in south-eastern Tasmania from sectioned otoliths, *(2)* describe the trends in sex-specific size compositions from these shelf waters, *(3)* examine spatial patterns in age composition between Storm Bay and east coast shelf waters and across the shelf, and *(4)* compare interannual trends in age composition to assess the extent of recruitment variability.

Methods

Study locality and sampling regime

Length-frequency data and otolith samples of *Nemadactylus macropterus* were obtained primarily from research sampling conducted seasonally on the shelf of southern and eastern Tasmania between January 1993 and January 1995. Sampling was conducted on the east coast of Tasmania between the southern end of Marion Bay and Schouten I., and in Storm Bay (Fig. 1). The survey areas were stratified into three depth strata (inner-shelf, 10–50 m; mid-shelf, 50–100 m; and outer-shelf, 100–200 m) on the east coast, and the inner-shelf (10–50 m) and mid-shelf (50–100 m) in Storm Bay. Full details of shelf and nearshore sampling areas, research survey design, gear and biological sampling are presented in this issue (Jordan 2001). Additional mature *N. macropterus* were sampled from commercial trawl catches made in eastern Tasmania in April, September, November and December in 1994.

10.1071/MF99157 1323-1650/01/040651

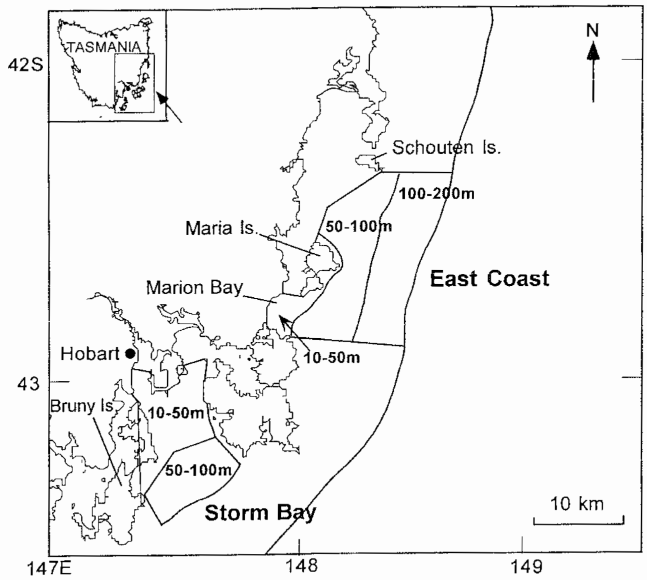


Fig. 1. Position of depth strata for shelf surveys on the east coast and Storm Bay, Tasmania.

Laboratory procedures

All fish processed for biological data were measured to the nearest millimetre fork length (FL) and weighed to the nearest gram. Sex was determined by macroscopic examination of the gonads. Sagittal otoliths of research shelf-caught *N. macropterus* were removed from a random sample of 20 fish in each depth stratum each season. Otoliths were removed from all fish caught from inshore surveys and commercial sampling. Once removed, otoliths were cleaned, dried, weighed to the nearest 0.001 gram and stored in envelopes prior to processing.

Sagittae were transversely sectioned through a three-stage process of embedding into polyester resin, sectioning to ~300 µm thick and mounting on glass slides. Transverse sections of sagittae from *N. macropterus* <12 cm were made by mounting the central part of the sagitta on the edge of 1-mm-thick glass slides with resin and grinding from anterior and posterior ends until a 1 mm section was obtained. Sections were then mounted on the surface of a glass slide and both surfaces ground with sequentially finer grades of carborundum paper until ~300 µm thick and viewed at either 12, 25 or 50 times magnification with a dissecting microscope with transmitted light and displayed on a personal computer. A customized image analysis system was used to enable on-screen digitizing and enhancing of each section.

Age estimates were derived by counting the presumed annual increments (opaque or dark zones) from the primordium to the edge of the otolith section on the ventral sector of the proximal side. Along this same axis the distances from the primordium to the outer edge of the first four opaque zones and to the edge of the section were measured to the nearest 0.1 µm. The opaque bands considered to be true annuli were distinguishable from false checks since they extended down both the ventral and dorsal sides of the medial groove and were continuous from the ventral edge to the sulcus. An increment was considered complete when a distinct opaque band was visible across the proximal face of the otolith section immediately inside a narrow discernible edge of translucent material. All counts and measurements of increments were made without knowledge of fish size, sex or date at capture. A total of 16% of otoliths was rejected because of the poor quality of sections.

Precision of age estimates

To compare the precision of age estimates, a random subsample of 100 sagittae was read a second time by the main reader, and by a second reader experienced in the reading of transverse sagittal sections. The average percent error (APE) was calculated for both the within- and between-reader age estimates from the formula of Beamish and Fournier (1981):

$$\mathrm{APE} = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{\left|X_{ij} - X_j\right|}{X_j}\right]$$

where N is the number of fish aged, R is the number of times fish are aged, X_{ij} is the ith determination of the jth fish and X_j is the average estimated age of the jth fish.

In addition, the percentage agreement of the within- and between-reader age estimates was calculated as another means of evaluating precision.

Growth

An absolute age was assigned to *N. macropterus* by using a birth date of 1 March, which corresponds to the mid-point of the spawning season in eastern Tasmania (Jordan 1998). Von Bertalanffy growth curves were then fitted to the individual length-at-age data for males and females separately and combined by direct non-linear least-squares estimation. To eliminate the bias of excluding slow growing juveniles that take longer to reach a size that can be sexed, juveniles were ranked by size, then each successive juvenile assigned an alternate sex and included in the calculation of the sex-specific von Bertalanffy growth curve.

The growth curves derived for males and females were compared by an F-test on the ratio of the mean square for the combined fit and the sum of the error mean square for males and females fitted separately (Ratkowsky 1983). Using the estimated ages, mean lengths at age were calculated for male and female *N. macropterus*, separately and combined.

Age composition

The size compositions of male and female *N. macropterus* from Storm Bay and the east coast were firstly obtained separately by pooling lengths from all seasonal research samples. The sex-specific size composition of the total population vulnerable to the sampling gear for both areas combined was then determined from the formula of Davis and West (1992) as described elsewhere in this issue (Jordan 2001).

The age composition of the population was then estimated for the 1994 research samples, with the number of fish aged proportional to the number of fish in each 2 cm size-class from the scaled population size composition of the same year. Year-class distributions were also examined for 1994, with the year-class referring to the year in which the fish were spawned. Age composition of the research-sampled shelf population was also examined by depth strata, with the number of fish aged proportional to the number in each 2 cm size-class from the scaled population size composition in each stratum across years.

Results

Size and sex compositions

Length–frequency distributions for all shelf surveys combined were determined separately for males and females (Fig. 2). Lengths ranged from 13.5 to 42.3 cm (mean 30.8 cm) for males and from 13.5 to 45.5 cm (mean 33.3 cm) for females. Although the distribution of both sexes was dominated by a single mode at around 33–4 cm, there was a

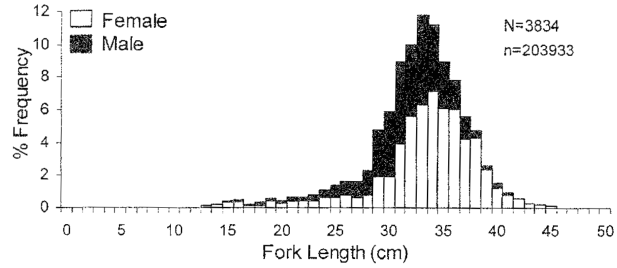


Fig. 2. Scaled length–frequency distributions of male and female *Nemadactylus macropterus* on the shelf region of southern and eastern Tasmania. N is measured sample size; n is scaled sample size.

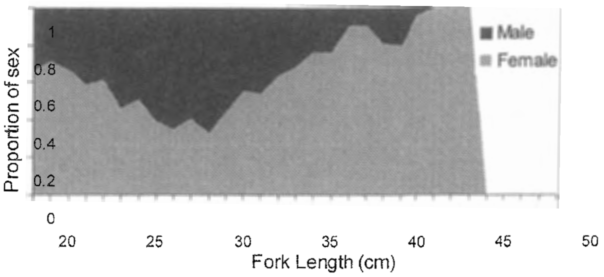


Fig. 3. Proportion of male and female *Nemadactylus macropterus* >20 cm by 1 cm length-class from the shelf region of southern and eastern Tasmania.

significant difference in the overall composition between sexes (Kolmogorov–Smirnov test, $P<0.001$), with considerably more large females than males. This is reflected in the fact that ~44% of females were above 35 cm, compared with 18% of males.

Sex ratios were determined for *N. macropterus* >20 cm, with the proportion of females significantly higher than males in autumn and winter in both 1993 and 1994 (Table 1). In all other seasons, sex ratios did not differ from 1:1. Sex ratios varied considerably by size-class, with females dominant between 20 and 24 cm and above 34 cm, and males dominant between 27 and 31 cm (Fig. 3).

Otolith structure and interpretation

Transverse sagittal sections of *N. macropterus* showed clear and distinctive alternating opaque and translucent zones seen under transmitted light (Fig. 4). The increment banding pattern remained relatively easy to read in older fish despite the narrowing of translucent zones. The primordial area of all otoliths consisted of a broad opaque zone with no obvious increment structure with a mean radius (± s.d.) of 502.0 ± 21.6 µm. It was visible in 58% of all sagittae examined, becoming less discernible with increasing age. A narrow band of poorly defined translucent material occurred outside this zone, adjacent to a second broad opaque zone visible in 89% of all sagittae with a mean radius of 680.0 ± 29.7 µm (Fig. 4). The structure of the otolith differed outside this second zone, with all sagittae of sufficient radius having a consistent narrower opaque zone with a mean radius of 922.3 ± 18.8 µm. Beyond this, there were clear and distinctive alternating opaque and translucent zones decreasing slightly in width towards the margin.

Given the variability in the structure of the opaque zones in the primordial region of the sagittae, the first annual increment was defined by comparing the seasonal progression of mean lengths of the 0+ and 1+ cohorts and the corresponding otolith radius. The radius from the primordium to the edge of the sagittal section on the ventral sector of the proximal side was measured from a representative subsample of these cohorts.

Progressions of size-compositions for *N. macropterus* <25 cm show 0+ fish first appearing in September. By October the mean length was ~7.7 cm, progressing through to 9.1 cm by January (Fig. 5). Given the arbitrary birthdate of 1 March, the cohort with a mean length of 11.8 cm in April represents the 1+ age-class. This cohort had progressed to a mean length of 20.1 cm by the following January and 20.8 cm by April, therefore representing the 2+ age-class.

The mean otolith radius of the 0+ cohort in October was 520 µm, which is only slightly greater than the mean radius of the first broad opaque zone (502 µm), suggesting that this zone forms immediately prior to, or during, settlement. The otolith radius increased to 601 µm by January and 778 µm by April, indicating that the second broad opaque zone (680 µm) is formed in late summer and is consistent with being the first annual increment. By the following January, the cohort with a mean length of 20.1 cm had a mean otolith radius of 996 µm, a radius consistent with the third narrower opaque zone (922.3 µm) visible in the primordial region of the sagittae, and hence defined as the second annual increment. This also indicates that new translucent material first appears in early summer (December).

Table 1. Sex ratios of *Nemadactylus macropterus* based on proportion of female (prop. F) by season

P is probability of sex ratios varying from 1:1 based on χ^2 tests. *n* is female scaled sample size

	1993				1994			1995
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Summer
prop. F	58.0	69.9	64.2	53.5	49.9	66.3	74.4	52.1
P	>0.05	<0.01	<0.01	>0.1	>0.5	<0.01	<0.01	>0.5
n	46763	24748	803	18511	39331	20354	55995	35118

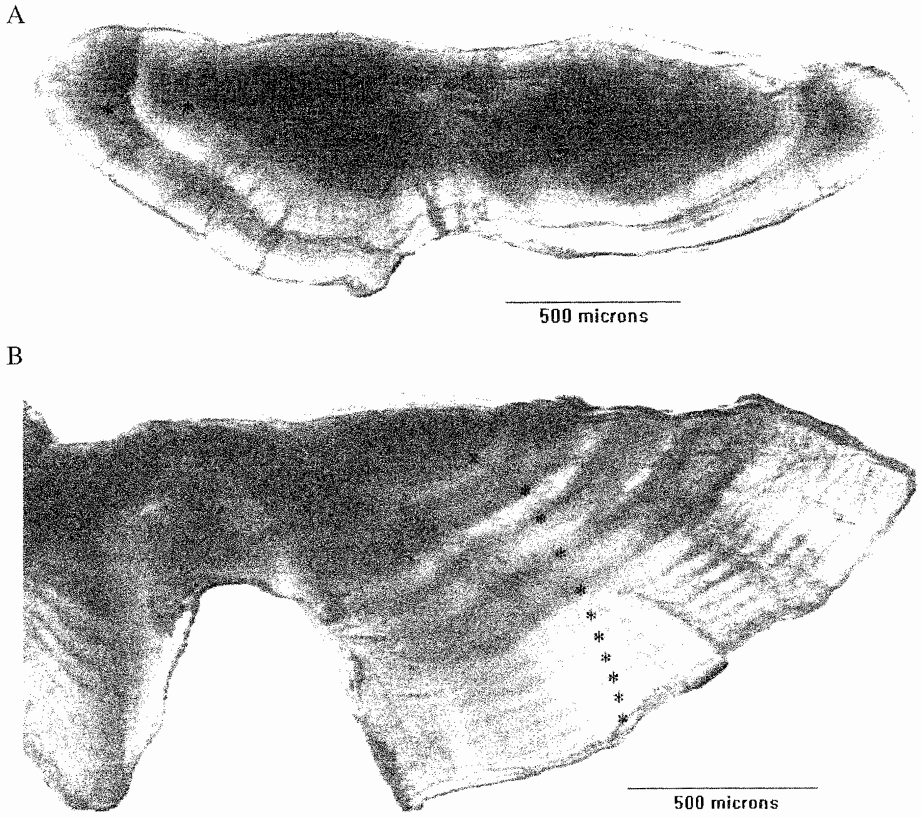


Fig. 4. Transverse sections of sagittal ogoliths of *Nemadactylus macropterus* viewed with transmitted light: *(A)* 2 year old and *(B)* 10 year old. Annual increments marked as *; inner increments seen in 58% of otoliths marked as **x**.

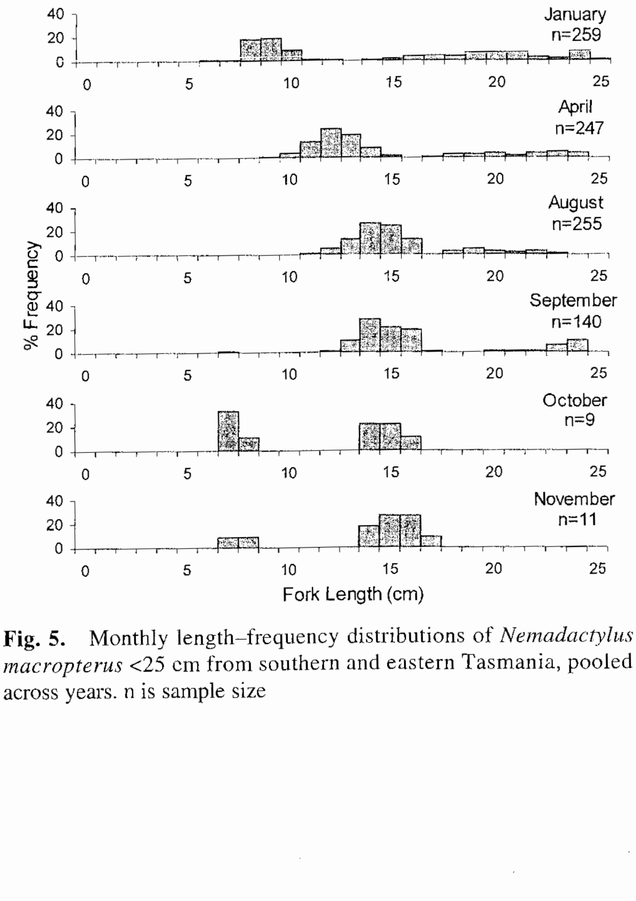


Fig. 5. Monthly length–frequency distributions of *Nemadactylus macropterus* <25 cm from southern and eastern Tasmania, pooled across years. n is sample size

Precision of age estimates

The index of average percent error (APE) calculated for repeat readings by the main reader was 0.25%, indicating a high consistency of similarity between readings. This is also reflected in the distributions of differences, with 92% of first and second readings the same. The differences are evenly distributed, indicating that there was no pattern of assigning consistently higher or lower estimates on the second reading. The index of APE for estimates between the main and second reader was higher at 2.23%, reflecting less consistency between readers. Age estimates between readers were the same 64% of the time, with evidence of the second reader assigning overestimates of age by one year in 19% of fish, compared with underestimates of one year in ~10%.

Growth

Mean lengths-at-age for male and female *N. macropterus*, separately and combined, are presented in Table 2. The mean length of females is consistently higher than that of males for all age classes up to 19 years, this last estimate consisting of only one fish. Von Bertalanffy growth curves

Table 2. Mean lengths at age (± s. d.) for the first 26 age-classes of male and female *Nemadactylus macropterus*, separately, and combined from southern and eastern Tasmania

n is sample size

Age	Females, males, juveniles			Females, juveniles			Males, juveniles		
	n	Mean	s.d.	*n*	Mean	s.d.	*n*	Mean	s.d.
1	9	14.47	1.88	9	14.47	1.88	7	14.61	2.15
2	8	22.06	3.04	6	21.73	3.16	3	21.73	3.35
3	10	28.03	1.82	2	28.10	1.27	5	27.58	1.83
4	16	31.16	1.64	11	30.81	1.44	5	31.92	1.96
5	27	32.34	2.09	19	32.48	2.36	8	32.01	1.35
6	42	33.60	1.67	23	33.76	1.83	19	33.42	1.48
7	23	33.04	2.55	13	33.79	2.00	7	32.51	3.24
8	6	33.60	2.39	4	34.30	1.64	2	32.20	3.82
9	9	34.83	2.94	5	35.68	2.33	4	33.78	3.63
10	4	35.48	1.19	3	36.03	0.50	1	33.80	
11	13	35.86	2.26	8	37.15	1.91	5	33.80	1.76
12	6	35.67	2.31	4	35.53	2.94	2	35.95	0.78
13	2	36.20	1.41	2	36.20	1.41	0		
14	3	34.20	3.41	1	35.70		2	33.45	4.46
15	6	38.38	2.90	4	39.93	2.07	2	35.30	0.85
16	5	37.06	3.34	5	37.06	3.34	0		
17	5	35.68	3.81	3	37.67	3.72	2	32.70	0.85
18	3	37.60	0.40	2	37.75	3.54	1	37.30	
19	3	35.47	0.76	1	36.00		2	35.20	0.86
20	1	38.20		0			1	38.20	
21	1	39.10		1	39.10		0		
22	1	40.30		1	40.30		0		
23	4	37.45	2.38	0			4	37.45	2.38
25	2	36.80	2.69	0			0		
26	1	42.60		1	42.60		2	36.80	2.69

were fitted to male and female individual length-at-age data separately (Fig. 6) and combined. Although there was no significant difference in the growth curves between males and females ($F = 2.33$, df 3,303, $P{>}0.05$), the distribution of lengths-at-age, particularly between 7 and 12 years, suggests some difference in growth between sexes. The lack of significance may result from the large number of juveniles and relatively few large, older fish in the samples. Hence, the sex-specific von Bertalanffy growth parameters are presented in Table 3. The asymptotic lengths (L_∞) for males and females were 36.2 cm and 38.4 cm, respectively.

There was a broad range of lengths within individual age-classes, with a maximum of 12 age-classes present in a 1 cm length-class. Growth in both sexes is rapid until ~5 years old (32–35 cm), and then slows appreciably. The maximum age for females was 30 years, whereas the oldest male examined was 41 years, although the next oldest male was 26 years old.

The relationship between fork length (cm) and weight (g) for *N. macropterus* is shown in Fig. 7. Slopes of the regression of log weight against log length for males and females were not significantly different (ANCOVA,

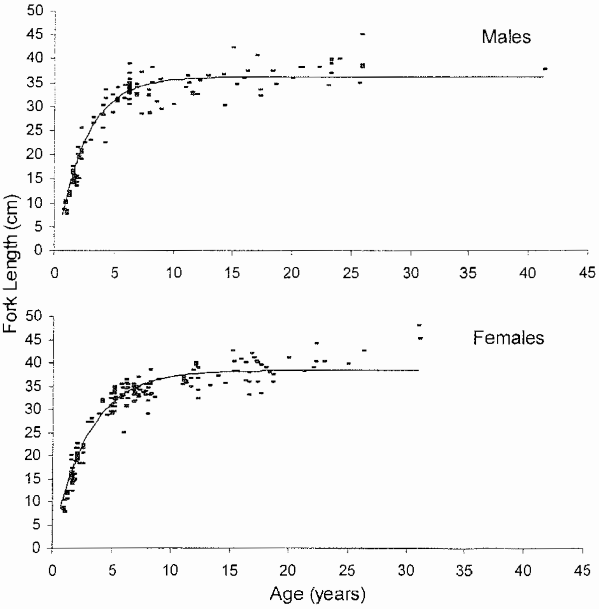


Fig. 6. Fitted von Bertalanffy growth curves for male and female *Nemadactylus macropterus* from southern and eastern Tasmania.

Table 3. von Bertalanffy growth parameters derived from length-at-age data for *Nemadactylus macropterus* from southern and eastern Tasmania

n is sample size

	von Bertalanffy growth parameters						
	n	L_∞	s.e.	*K*	s.e.	t_0	s.e.
All	316	37.41	0.28	0.37	0.02	0.40	0.07
Females/juveniles	184	38.44	0.36	0.33	0.02	–0.07	0.09
Males/juveniles	127	36.16	0.43	0.42	0.03	0.15	0.10

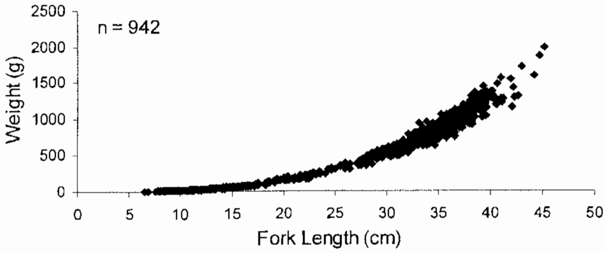


Fig. 7. Relationship of fork length against weight for *Nemadactylus macropterus* from southern and eastern Tasmania.

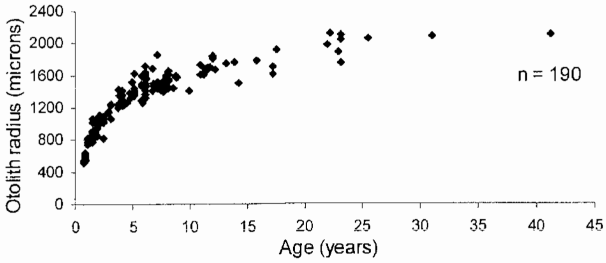


Fig. 8. Relationship of otolith radius against age for female and male *Nemadactylus macropterus* from southern and eastern Tasmania.

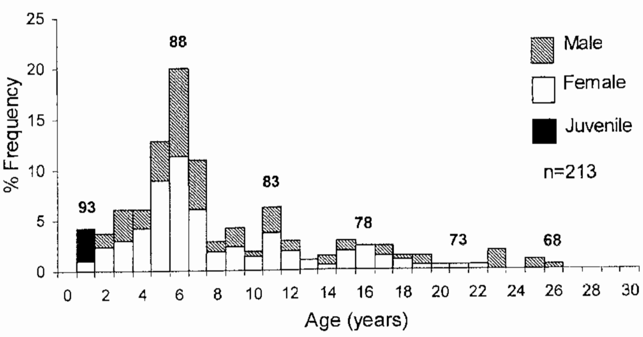


Fig. 9. Estimated age composition of*Nemadactylus macropterus* from the shelf region of southern and eastern Tasmania in 1994. Year-class is provided above the age frequency for every fifth year. n is sample size.

$F = 1.95$, df 1,602, $P>0.1$) and there was no significant difference in the intercepts for the two sexes (ANCOVA, $F = 0.66$, df 1,603, $P>0.1$). Hence, both sexes and juveniles were combined to determine the relationship between length (cm) and weight (g) (Table 4).

The relationship between otolith radius and age was examined separately for male and female *N. macropterus*, and combined (Fig. 8). Residuals from the linear regressions show considerable increase in variance in otolith radius with increasing age, with a distinct curvilinear relationship apparent for both sexes. The regression of log otolith radius against log age was not significantly different for males and females (ANCOVA, $F = 1.94$, df 1,190, $P>0.1$), so the relationship was calculated for both sexes combined (Table 4).

Age composition

The population of male and female *N. macropterus* from shelf regions of southern and eastern Tasmania in 1994 contained a maximum of 19 and 22 age-classes of males and females, respectively, and was dominated by 5–7-year-old fish that made up 44% of the population (Fig. 9). There was no significant difference in the age composition of males and females (KS test, $P > 0.8$). The high proportion of 6 year olds in the population in 1994, representing the 1988 year-class, indicates that strong recruitment occurred in that year (Fig. 9). There is also some evidence of strong recruitment in 1983 and between 1977 and 1979, suggesting that variations in year-class strength may be a regular feature of the population of *N. macropterus* in southern and eastern Tasmanian shelf waters.

Table 4. Length (FL)–weight (WT) and otolith radius (OR)–age regressions for *Nemadactylus macropterus* from southern and eastern Tasmania

n is sample size

			$Y = a + bX$		
Y	*X*	*n*	*a*	*b*	r^2
$\log_{10}$WT	$\log_{10}$FL	941	–1.841	3.086	0.99
Female/male					
$\log_{10}$OR	$\log_{10}$AGE	190	2.879	0.338	0.91

Comparison of age compositions across depth strata in Storm Bay reveals that the area was dominated by one-year-old *N. macropterus*, with little evidence of depth preference of juveniles (Fig. 10). Although few mature fish were present in Storm Bay, all were caught in the mid-shelf stratum. The age structure of fish on the east coast differed substantially from those in Storm Bay, with the inner shelf consisting exclusively of 0+ fish (Fig. 10). In contrast, mid- and outer-shelf strata were dominated by older age-classes, with no evidence of age-structuring between strata as fish were evenly distributed across these depths.

Discussion

Otolith structure

Increment structure of sagittal sections of *N. macropterus* otoliths consisted primarily of clear and distinctive alternating opaque and translucent zones, with a narrowing of translucent zones with increasing age. The structure of the two innermost opaque zones, however, differed from those outside this region, being broader and poorly defined, particularly in older fish. By comparing the progression of mean lengths of the 0+ and 1+ cohorts and otolith radius, the first of these two zones was found to be formed immediately prior to, or during, settlement. The mark is consistent with the opaque zone that forms during post-larval metamorphosis of *N. macropterus* in New Zealand (Vooren 1972). The second broad opaque zone became discernible by February and is consistent with being the first annual increment. The third opaque zone was narrower than the inner two, being visible inside a narrow edge of translucent material by January and is consistent with being the second annual increment. The close correspondence between increment radius and modal lengths of juveniles confirms that one increment is formed each year, at least for the first 2 years. Although increments in older fish were clear and unambiguous, further validation is required as older age-classes have only been validated through analysis of trends in marginal increments in whole otoliths (Smith 1982).

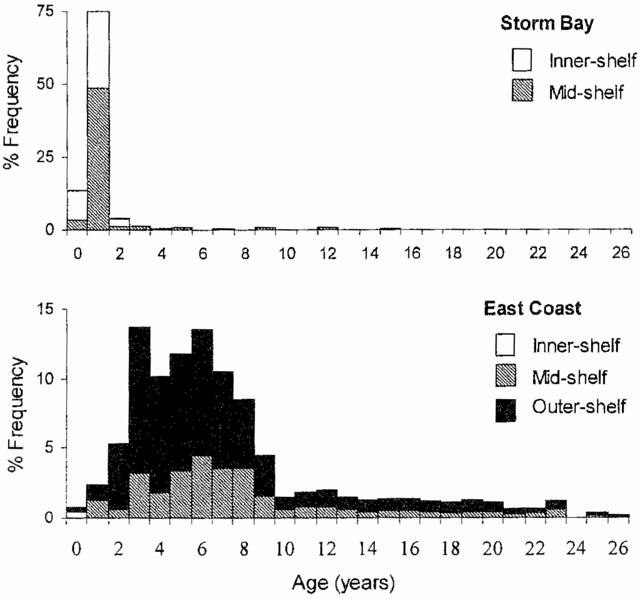


Fig. 10. Age composition of *Nemadactylus macropterus* from inner and mid-shelf regions of Storm Bay and inner, mid- and outer-shelf regions of the east coast between 1993 and 1995.

The first annual increment was visible in most otoliths, although it became more poorly defined with increasing age because of later deposits of opaque material obscuring the region of the primordium. The presence of a dense opaque zone around the primordium, check marks, and decreases in the width of opaque zones with increasing age in many species often results in difficulty in identifying the first several annuli (Chilton and Beamish 1982; Fowler and Doherty 1992). Vooren (1972) found the first two increments in whole sagittae of *N. macropterus* to be less clear with increasing age, suggesting that the diameter of the innermost rings be measured to reduce underestimates of age. The present study indicates that such underestimates can also occur in transverse sagittal sections and hence measurements of inner increments should be routinely made, regardless of the method of otolith preparation.

Growth

Growth in *N. macropterus* is rapid for the first 3 years, reaching approximately 12, 20 and 26 cm after 1, 2 and 3 years, respectively. This size-at-age is consistent with that previously reported from south-eastern Tasmania, based on modal progressions of juvenile cohorts (Smith 1989). The seasonal progression of these age-classes indicates that most growth occurs during summer and autumn when water temperatures on the shelf of southern and eastern Tasmania are at a maximum (Harris *et al.* 1991). The inclusion of considerable numbers of juveniles resulted in values for t_0 for males and females being 0.15 and –0.07, respectively, suggesting that the von Bertalanffy growth curve is a reasonably good representation of juvenile growth. After 3–4 years there was an increasing variation in size-at-age, with fish at a length of 30 cm ranging from 5 to 15 years old.

The maximum ages for female and male *N. macropterus* were 30 and 41 years, respectively. The difference of 15 years between the oldest and second oldest male indicates that a larger number of fish may need to be aged in order to adequately sample the older fish in the population. The maximum ages in this study are considerably higher than those reported for male and female *N. macropterus* from New South Wales and north-eastern Victoria at 11 and 16 years, respectively (Smith 1982), and eastern Bass Strait at 11 and 13 years, respectively (Wankowski *et al.* 1988). The higher maximum ages of *N. macropterus* from Tasmania may reflect spatial variations in size and age structure and/or underestimates of age in older fish by Smith (1982) and Wankowski *et al.* (1988) because of the use of whole sagittal otoliths.

With regard to the former hypothesis, the size composition of fish from southern New South Wales ranged from 22 to 47 cm, with most individuals between 27 and 37 cm (Smith 1983), which is consistent with the present study for fish from eastern Tasmania. Such size compositions are also evident in eastern Bass Strait in more recent years (Smith 1995). Seasonal variability in abundance also suggests some movement of fish between eastern Tasmania and eastern Bass Strait (Jordan 1998), indicating that age differences may not result from spatial differences in growth. The more likely explanation for the differences would appear to be that ages were underestimated, a conclusion that is consistent with previous studies where age estimates were lower from whole otoliths compared with those sectioned or broken and burnt (Beamish 1979; Collins *et al.* 1988; Hyndes *et al.* 1992). It is also consistent with a recent reappraisal of ages of *N. macropterus* from south-eastern Australia, from sectioned otoliths, where maximum ages of 31 and 38 years were estimated for males and females, respectively (Morison 1996). A similar maximum age of 41 years has been derived for New Zealand based *N. macropterus* from examination of broken and burnt sagittae (Vooren 1977). Although maximum age of *N. macropterus* in Australian waters is higher in the present study than previously derived, mean length-at-age for 3–5 year olds is similar to those of Smith (1982), indicating that underestimates of age are restricted to older age-classes because of the narrowing of increments. This is consistent with the relationship between age and otolith length where increases in otolith length slowed with increasing age.

Although there was no significant difference in the growth curves between sexes, the larger lengths-at-age for females between 7 and 11 years suggest that growth is faster for females in certain age-classes. The lack of significance may result from the small number of 3–5 year olds, large number of juveniles and relatively few large, older fish in the samples. Smith (1982) found faster growth in females, although the lower K values of 0.13 and 0.17 for females and males, respectively, can be attributed to underestimates of age through the use of whole otoliths. Recent estimates of growth parameters of *N. macropterus* from ages derived from sectioned otoliths (Tilzey 1999) are similar to those in the present study.

Despite some evidence of sex-specific growth rates, the differences are unlikely to result in the predominance of females above 34 cm. This conclusion is consistent with Smith (1983) who considered growth differences to be insufficient to account for the predominance of females among the larger size-classes of *N. macropterus* off New South Wales and attributed it to increased mortality of older males. Such differential mortality may explain the higher proportion of females in the older age-classes in the present study. Although recent estimates of total mortality from sectioned otoliths are considerably lower (0.18) (Tilzey 1999) than previously derived (0.6–0.77) (Smith 1995), the lack of sex-specific mortality estimates precludes an assessment of the significance of such differences in structuring the sex composition of the population.

Spatial and temporal patterns in age composition

The present study revealed distinct differences in the age composition of *N. macropterus* between Storm Bay and the east coast, with very few fish older than 2+ present on the mid-shelf of Storm Bay compared with the east coast. The absence of sampling in the outer-shelf stratum in Storm Bay precludes a comparison of the age structure of these depths between areas. However, the results clearly indicate that the inner- and mid-shelf waters (10–100 m) of Storm Bay are primarily a nursery area for the species, fish moving out of this area at ~3 years old with the onset of maturity. This is consistent with *N. macropterus* in New Zealand that also recruit to distinct nursery areas in depths of 20–100 m until age 3 (Vooren 1975). In contrast, whereas the inner-shelf on the east coast consisted exclusively of 0+ fish, the mid- and outer-shelf contained both juveniles and mature fish. Therefore, not all juveniles are restricted to shallow distinct nursery areas, and so age-specific migrations are apparent for only a portion of the population. The effects of these spatial differences in age composition should be taken into consideration when incorporating size-dependent depth distributions into stock assessments for *N. macropterus*.

The estimated age composition of *N. macropterus* in southern and eastern Tasmania in 1994 consisted of a maximum of 19 and 22 age-classes of males and females, respectively, and was dominated by 5–7-year-old fish. The high proportion of 6 year olds in 1994, representing the 1988 year-class, suggests that strong recruitment occurred in that year. However, the relative abundance of this age-class will be strongly influenced by its catchability in the demersal trawl gear relative to others, particularly younger age-classes. In estimating the age composition of *N. macropterus* in eastern Bass Strait, Wankowski *et al.* (1988) considered 3 year olds to be fully recruited to demersal trawl gear with similar mesh configurations to that used in the present study. This is supported by lengths at 50% selection for *N. macropterus* in 90 mm mesh ranging from 20 to 23 cm (Han 1964), and in 100 mm mesh of ~24 cm (2+ fish) (Massey 1988). Hence, the use of 20 mm codend mesh in the present study resulted in 3 year olds (~28 cm) being fully recruited to the trawl gear and therefore representatively sampled.

The relative abundance of age-classes will also be influenced by differences in age structure resulting from variations in the spatial pattern of recruitment and migration. Despite evidence of interannual variations in the distribution of settlement between Storm Bay and the east coast (Jordan 1998), larger juveniles are known to show considerable movement at much larger spatial scales than examined in the present study, as 3-year-old *N. macropterus* move into shelf regions of southern New South Wales from nursery areas in Tasmania (Smith 1989). Therefore, some movement of larger juveniles can be expected between Tasmanian shelf regions, which is consistent with the absence of 3 year olds in Storm Bay. Although the migration of larger juveniles from Tasmanian nursery areas would result in a decrease in the abundance of such age-classes in these waters, there is uncertainty regarding the extent of movement from the south-east Tasmania shelf region. This is reflected in the uncertainty in the stock structure of *N. macropterus* throughout southern Australia, with allozyme and mitochondrial DNA studies suggesting the presence of a single stock in these waters (Elliot and Ward 1994; Grewe *et al.* 1994). Otolith microchemistry analysis, however, indicates that distinct stocks occur in both Tasmania and New South Wales/Victoria, with mixing rates low but sufficient to result in genetic convergence of samples (Thresher *et al.* 1994).

Despite the uncertainty regarding the extent of mixing throughout south-eastern Australia, there are few differences in the size composition of mature *N. macropterus* in south-eastern Tasmania and New South Wales (Smith 1983) that would result from a consistent, directional movement of fish. Therefore, the relative contribution of 6-year-old fish is unlikely to be biased and therefore indicates strong recruitment of the 1988 year-class. Evidence of strong recruitment is also present in 1983 and between 1977 and 1979, suggesting that variations in year-class strength are a consistent feature of the *N. macropterus* population in eastern Tasmania. The age composition of *N. macropterus* in New South Wales/ Victoria waters also shows evidence of recruitment variability, with some indication of strong year-classes every 4–5 years (Tilzey 1999). An increased abundance of 3+ fish on the shelf of New South Wales in 1979–80 led Smith (1989) to suggest that there was strong recruitment of the 1977 and 1978 year-classes. The evidence of these strong year-classes in the present data clearly suggests that year-class variations are present across the species distribution in south-eastern Australia.

There is evidence that recruitment variations may be driven by interannual variations in the local hydrography that to some extent determine the supply of post-larval *N. macropterus* into inner- and mid-shelf waters (Jordan 2001). This hypothesis is supported by the fact that the settlement period of 1988–89 was characterized by a reduction in the westerly wind stress, resulting in a persistent onshore flow of subtropical EAC water onto the shelf of south-eastern Tasmania associated with a major El Niño/Southern Oscillation (ENSO) event in that year (Harris *et al.* 1991). If the supply of post-larvae is strongly influenced by transport processes, then the reduction in westerlies in late 1988 may have provided optimum conditions for onshore movement of fish onto the inner- and mid-shelf through passive transport, active horizontal swimming, or a combination of the two. What is particularly noteworthy is the similarity in the timing of reductions in westerly winds and good recruitment in *N. macropterus*, with evidence of strong year-classes in the period around 1978, coincident with reduced westerlies in those years (Harris *et al.* 1988). It is clear that in order to further examine the factors driving recruitment variations in *N. macropterus*, detailed studies are needed on the hydrography of offshore and shelf waters of south-eastern Australia and its influence on post-larval supply.

Acknowledgments

I gratefully acknowledge the assistance of the captain and crew of FRV *Challenger* without whose help the shelf sampling would not have been possible. Thanks also go to the many staff of the Marine Research Laboratories, including Carl Waterworth, Wes Ford, Tristan Richards, Fiona Ewing, Ray Murphy, David Mills and Graeme Ewing, who provided assistance at sea and in the laboratory. The staff at the Central Ageing Facility provided valuable assistance with otolith preparations and readings. Thanks also to Jeremy Lyle, Robert White and Sandy Morison.

References

Beamish, R. J. (1979). Differences in the age of Pacific hake (*Merluccius productus*) using whole and sectioned otoliths. *Journal of the Fisheries Research Board of Canada* **36**, 141–51.

Beamish, R. J., and Fournier, D. A. (1981). A method of comparing the precision of a set of age determinations. *Journal of the Fisheries Research Board of Canada* **36**, 1395–400.

Chilton, D. E., and Beamish, R. J. (1982). Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences No. 60. 102 pp.

Collins, M. R., Schmidt, D. J., Waltz, C. W., and Pickney, J. L. (1988). Age and growth of the king mackerel, *Scomberomorus cavalla*, from the Atlantic coast of the Unites States. *Fishery Bulletin (US)* **87**, 49–61.

Davis, T. L. O., and West, G. J. (1992). Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the north west shelf of Australia. *Fishery Bulletin (US)* **90**, 395–404.

Elliot, N. G., and Ward, R. D. (1994). Enzyme variation in jackass morwong, *Nemadactylus macropterus* (Schneider, 1801) (Teleostei: Cheilodactylidae), from Australian and New Zealand waters. *Australian Journal of Marine and Freshwater Research* **45**, 51–67.

Fowler, A. J., and Doherty, P. J. (1992). Validation of annual growth increments in the otoliths of two species of damselfish from the southern Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* **43**, 1057–68.

Grewe, P. M., Smolenski, A. J., and Ward, R. D. (1994). Mitochondrial DNA diversity in jackass morwong (*Nemadactylus* *macropterus*: Teleostei) from Australian and New Zealand waters. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1101–9.

Han, V. C. F. (1964). Studies on the biology of the jackass fish, *Nemadactylus macropterus* Bloch and Schneider (1801). M.Sc. Thesis, University of Sydney, Australia.

Harris, G. P., Davies, P., Nunez, M., and Meyers, G. (1988). Interannual variability in climate in Tasmania and its effect on freshwater and marine fisheries. *Nature* **333**, 754–7.

Harris, G. P., Griffiths, F. B., Clementson, L. A., Lyne, V., and Van der Doe, H. (1991). Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. *Journal of Plankton Research* **13** Suppl., 109–31.

Hyndes, G. A., Loneragan, N. R., and Potter, I. C. (1992). Influencing of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. *Fishery Bulletin (US)* **90**, 276–84.

Jordan, A. R. (1998). The life-history ecology of *Platycephalus bassensis* and *Nemadactylus macropterus*. PhD Thesis. University of Tasmania, Hobart, Australia.

Jordan, A. R. (2001). Spatial and temporal variations in abundance and distribution of juvenile and adult jackass morwong, *Nemadactylus macropterus*, in Tasmania. *Marine and Freshwater Research* **52**, 661–70.

Massey, B. R. (1988). Trawl mesh selection of some important commercial fish species in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **22**, 75–84.

Morison, A. K. (1996). 'Age and growth of major species in the South East Fishery.' (The Central Ageing Facility Marine and Freshwater Resources Institute, Department of Natural Resources and Environment: Queenscliff, Vic.)

Ratkowsky, D. (1983). 'Nonlinear Regression Modelling.' (Marcel Dekker, Inc:, New York, NY.) 276 pp.

Smith, D. C. (1982). Age and growth of jackass morwong (*Nemadactylus macropterus* Bloch and Schneider) in eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **33**, 245–53.

Smith, D. C. (1983). Annual total mortality and population structure of jackass morwong (*Nemadactylus macropterus*, Bloch and Schneider) in eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **33**, 253–60.

Smith, D. C. (1989). The fisheries biology of jackass morwong (*Nemadactylus macropterus* Bloch and Schneider) in south-eastern Australian waters. PhD Thesis University of New South Wales, Australia.

Smith, D. C. (1995). Jackass morwong 1994. Stock Assessment Report, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Thresher, R. E., Proctor, C. H., Gunn, J. S., and Harrowfield, I. R. (1994). An evaluation of electron-probe microanalysis of otoliths for stock identification of nursery areas in a southern temperate groundfish, *Nemadactylus macropterus* (Cheilodactylidae). *Fishery Bulletin (US)* **92**, 817–40.

Tilzey, R. D. J. (Ed.) (1999). The South East Fishery 1998. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Vooren, C. M. (1972). Postlarvae and juveniles of the tarakihi (Teleostei: Cheilodactylidae) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **6**, 602–18.

Vooren, C. M. (1975). Nursery grounds of tarakihi (Teleostei: Cheilodactylidae) around New Zealand. *New Zealand Journal of Marine and Freshwater Research* **9**, 121–58.

Vooren, C. M. (1977). Growth and mortality of tarakihi (Teleostei: Cheilodactylidae) in lightly exploited populations. *New Zealand Journal of Marine and Freshwater Research* **11**, 1–22.

Wankowski, J. W., Hyduke, E., and Williams, S. (1988). Population age structure and mortality rates of jackass morwong (*Nemadactylus macropterus*) in Eastern Bass Strait, Australia. *Fisheries Research* **6**, 317–35.

Manuscript received 5 November 1999; revised and accepted 24 February 2000

Mar. Freshwater Res., 2001, **52**, 661–70

Spatial and temporal variations in abundance and distribution of juvenile and adult jackass morwong, *Nemadactylus macropterus*, in south-eastern Tasmania

Alan R. Jordan

Marine Research Laboratories, Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Crayfish Point, Taroona, Tas. 7053, Australia

Abstract. Depth-stratified random demersal trawl surveys of the shelf of southern and eastern Tasmania from summer 1993 to summer 1995 showed seasonal variations in abundance of *N. macropterus* in all depth strata, although the trend varied between years, with abundance peaking in summer 1993 and winter 1994. This variation is attributed to the seasonal movement of fish from south-eastern Tasmanian shelf waters, although some seasonal change in size composition is also evident. Catch rates were highest on the outer shelf and lowest on the inner shelf, reflecting the distinct size-structuring, with juveniles concentrated on the inner and mid shelf and mature fish on the outer shelf. Size compositions differed among shelf regions, with few mature fish on the mid shelf of Storm Bay compared with the same stratum on the east coast, indicating that the bay is primarily a nursery area for the species. Settlement from the pelagic post-larval phase occurred in spring and early summer at 7–9 cm, with evidence of movement between inner- and mid-shelf strata by autumn. Abundance of 0+ fish was highest in 1993 and 1994 and a considerable decrease in the abundance in both regions in 1995. The influences of local hydrography and the large size at settlement are discussed.

Introduction

Jackass morwong (*Nemadactylus macropterus*) is a demersal species commonly found in coastal and continental shelf waters of southern Australia, New Zealand and South America. It is an important commercial species in the South East Fishery, with the bulk of landings taken off southern New South Wales, eastern Bass Strait and eastern Tasmania by both Danish seiners and otter trawlers (Smith 1994). Despite lower catches in recent years, they continue to be an important commercial species with 1206 t landed in 1997 (Tilzey 1999). In Tasmanian inshore waters, *N. macropterus* are caught mainly by otter trawl, although up to 10% are caught by gillnets. Recent landings in this fishery have ranged from around 137 t in 1990–91 to 19 t in 1996–97 (Lyle and Jordan 1998).

Distinct seasonal and spatial variations in the abundance of *N. macropterus* occur on the shelf of eastern Bass Strait, the variations being attributed to migration of fish into the area and seasonal changes in vulnerability because of spawning activity (Wankowski and Moulton 1986). Seasonal and depth variations in catch rate also occur across the entire South East Fishery, with abundances highest in the 100–149 m stratum in summer (Smith 1994). Catch rates of *N. macropterus* around Tasmania peak in depths of 150–199 m, reflecting the concentration of adult fish in those depths (Lyle and Ford 1993).

One of the main factors influencing the spatial variations in abundance of several demersal species on the shelf of south-eastern Tasmania is size structuring by depth, with juveniles inshore and adult fish in deeper water indicating a size- or age-specific migration from nursery areas to deeper adult grounds (Jordan 1998). There is also considerable seasonal and interannual variation in abundance for many species, reflecting the movement of fish out of the region (Jordan 1998). This is consistent with several demersal species on the New South Wales shelf where there is considerable seasonal movement of fish along the shelf (Graham *et al.* 1996). The presence of such spatial and temporal variability has important implications for the interpretation of catch data from the commercial fishery, as variations in size compositions and catch rates from the fishery may reflect shifts in effort across these scales rather than changes in the size composition or stock abundance

There is evidence that *N. macropterus* use discrete nurseries in south-eastern Australia as juveniles appear to be restricted to coastal waters of Bass Strait and Tasmania, and are rarely caught in eastern Victoria, New South Wales and the Great Australian Bight (Smith 1983; Lyle and Ford 1993). Distinct nursery areas have also been identified for *N. macropterus* in New Zealand waters, with juveniles restricted to the inner-shelf (Vooren 1975). Settlement into south-eastern Tasmanian shelf waters occurs in summer at

10.1071/MF99156 1323-1650/01/040661

around 7–8 cm (Lyle and Ford 1993), after an extended larval period concentrated in offshore waters of south-eastern Australia (Bruce *et al.* 2001). This is consistent with the size and timing of settlement into nursery areas in New Zealand (Vooren 1972) where there is also evidence of interannual variability in the abundance of 0+ fish recruiting to individual nursery areas (Vooren 1975).

Although juveniles appear to be restricted to inner-shelf waters of Tasmania (Lyle and Ford 1993), these results are likely to be biased as these surveys were unstratified and used Danish seine and otter board trawlers in different depths with differing fishing power, net designs and mesh size. By using a stratified random survey design with a standardized research vessel and demersal trawl gear, this research aims to confirm the depth-related variations in catch rates and size compositions of Lyle and Ford (1993). In addition, to better understand the factors influencing the temporal and spatial structure of the *N. macropterus* population, the seasonal, interannual and spatial patterns of abundance of juveniles and adults on the shelf of southern and eastern Tasmania are examined.

Methods

Study locality and sampling regime

Nemadactylus macropterus were sampled seasonally on the shelf of eastern and south-eastern Tasmania in eight out of the nine seasons between summer 1993 and summer 1995. Demersal tows were made at random stations in three strata (inner-, 10–50 m; mid-, 50–100 m; and outer-shelf, 100–200 m) on the east coast of Tasmania between the southern end of Marion Bay and the southern end of Schouten Island, and two strata (10–50 m, 50–100 m) in Storm Bay (Fig. 1). Depth strata were allocated stations proportional to the area of the stratum with a maximum of 22 random stations on the east coast and 20 in Storm Bay. The east coast areas of Maria Island and Storm Bay were chosen as suitable continental shelf survey areas as they represented known areas of commercial trawl activity. From 1989 to 1992, ~75% of state inshore trawl catches came from these two areas (Lyle 1994), representing landings from the east coast and Storm Bay of around 260, 190, 255 and 315 t year^{-1}.

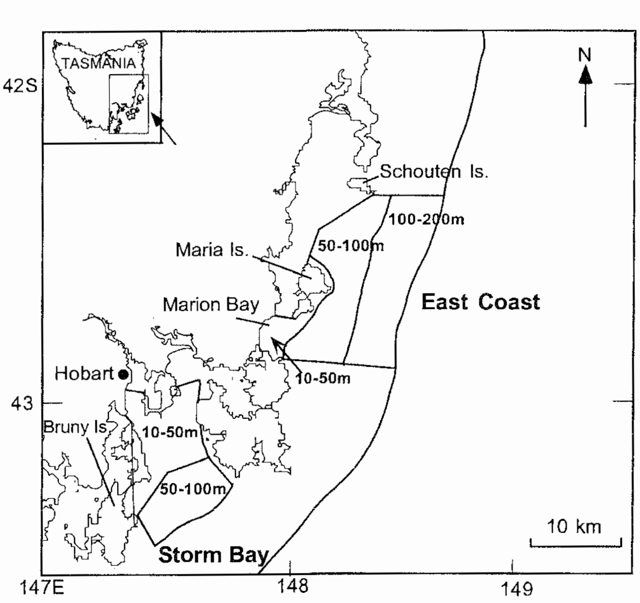


Fig. 1. Position of depth strata for shelf surveys on the east coast and Storm Bay, Tasmania.

At each station the net was towed for 30 min (bottom time) at a speed of 3.0 kn. When a constant warp length to bottom depth ratio is used, both wingspread and/or doorspread have been found to be greater with increasing depth. Hence, the ratio of warp length to bottom depth was increased from 3:1 in depths >150 m to around 8:1 in depths <40 m. The aim of varying the ratio was to gain the desired wingspread of 50% of headline length. Surveys were conducted from the FRV *Challenger*, a stern trawler with the following specifications: length 21.3 m; beam 5.85 m; gross tonnage 87 t; horsepower 500. Trawling was conducted with a demersal trawl with the following specifications: headline length 26 m; sweeps 38 m; bridles 25 m; wing mesh 120 mm; top and bottom panel mesh 100 mm; codend mesh 80 mm; and a 20 mm codend liner. The ground rope consisted of rubber bobbins and a steel danleno at each wingtip and was ~0.2 m off the bottom.

Tows less than 15 min were excluded from abundance and size composition estimates. Stations were abandoned if, after the trawl path was surveyed, the bottom proved unsuitable for trawling. Tows were conducted between sunrise and sunset. Total catch of *N. macropterus* at each station was weighed with either a 15 kg or 40 kg clock face scale (±0.1 kg) and all individuals were sampled for length (FL), a minimum of 100 of these by sex. Catch rates were calculated as the number of fish per tow (N tow^{-1}). Details of stratum area, numbers of stations sampled in each stratum in each season and station density for shelf surveys in Storm Bay and the east coast are presented in Table 1. Juvenile *N. macropterus* were also sampled from nearshore regions (0–12 m) at several sites in south-eastern Tasmania between October and December 1995 with both a 2.0 × 0.9 m beam trawl and 30 m multi-panel gillnets comprising three 10 m panels of increasing mesh size (64, 89 and 108 mm).

Statistical analysis

Spatial and temporal variations in the abundance of *N. macropterus* in Storm Bay and the east coast were assessed by analysis of variance (ANOVA). Variations in abundance (N tow^{-1}) were analysed for Storm Bay and the east coast separately by two-way ANOVA, with season and depth considered fixed factors. Analysis of variations in the abundance of *N. macropterus* from Storm Bay was restricted to juvenile size-classes, which made up around 94% of the population. Fish were classified as juveniles based on their fork length and macroscopic gonad staging. Due to heterogeneity of data from winter 1994 on the east coast, analysis of variations in the seasonal abundance of *N. macropterus* from that area was restricted to four seasons (summer–spring 1993). Interannual variations in abundance of mature *N. macropterus* on the east coast among the summers of 1993, 1994 and 1995 were assessed by two-way ANOVA, with year and depth considered fixed factors.

Before analysis, data were tested for conformity to the assumptions of ANOVA by the F_{max} test for heteroscedascity and by examining residual and normal probability plots. Transformation of abundance to $\ln(x+1)$ greatly improved the homogeneity of variances and distribution of residuals. Interannual variations in the abundance of 0+ *N. macropterus* in all three summers were to be assessed by ANOVA; however, as patchy distribution resulted in data remaining heterogeneous after transformation, the means were examined for trends. Ryans Q test was used to identify significant differences among means when there were significant main effects or interactions in the ANOVA because it is considered to be the most powerful post-hoc test that allows the user to control experiment-wise error rate (Day

Table 1. Details of stratum areas, number of stations and station density (N km^{-2}) for east coast (EC) and Storm Bay (SB) survey areas in each season

Year	Season	Region	Stratum	Area (km^2)	No. stations trawled	Station density
1993	Summer	EC	10–50	112	3	1/37
			50–100	565	16	1/94
			100–200	416	4	1/104
		SB	10–50	377	7	1/54
			50–100	383	10	1/38
1993	Autumn	EC	10–50	112	2	1/56
			50–100	565	11	1/52
			100–200	416	8	1/52
		SB	10–50	377	10	1/38
			50–100	383	8	1/48
1993	Winter	EC	10–50	112	2	1/56
			50–100	565	11	1/52
			100–200	416	6	1/69
		SB	10–50	377	9	1/42
			50–100	383	9	1/43
1993	Spring	EC	10–50	112	1	1/112
			50–100	565	8	1/71
			100–200	416	7	1/59
		SB	10–50	377	10	1/38
			50–100	383	10	1/38
1994	Summer	EC	10–50	112	1	1/112
			50–100	565	9	1/63
			100–200	416	7	1/59
		SB	10–50	377	10	1/38
			50–100	383	8	1/48
1994	Autumn	EC	10–50	112	1	1/112
			50–100	565	6	1/94
			100–200	416	5	1/83
		SB	10–50	377	8	1/47
			50–100	383	8	1/48
1994	Winter	EC	10–50	112	2	1/56
			50–100	565	9	1/43
			100–200	416	5	1/83
		SB	10–50	377	8	1/47
			50–100	383	8	1/48
1995	Summer	EC	10–50	112	2	1/56
			50–100	565	9	1/63
			100–200	416	8	1/52
		SB	10–50	377	8	1/47
			50–100	383	8	1/48

and Quinn 1989). Calculations were performed with the Peritz FORTRAN program (Martin and Toothaker 1989).

Size composition

Size compositions of *N. macropterus* vulnerable to the sampling gear were firstly obtained by pooling lengths from all random trawl stations in a stratum in each season in both Storm Bay and east coast survey areas. The size composition of the total population in each area, season and stratum was then estimated by weighting each size class by the number of tows relative to the stratum area, using the formula of Davis and West (1992):

$$F_i = \sum_{j=1}^{j=3} \mathrm{f}_{ij} \, A_j / n_j$$

where F_i is the relative frequency of size class i in the population, f_{ij} is the frequency of size class i in stratum j, A_j is the area of stratum j and n_j is the number of trawls in stratum j (see Table 1).

Results

Catch rates

Abundance of mature *N. macropterus* on the shelf of the east coast in 1993 varied significantly amongst seasons ($P<0.001$) and depths ($P<0.02$) (Fig. 2). Post-hoc tests revealed that abundances were significantly higher on the outer- and mid-shelf than on the inner-shelf (Ryans Q-test; $P<0.05$). Abundances were also significantly higher in summer, autumn and spring than in winter (Ryans Q-test; $P<0.05$). The significance of trends in abundance in 1994 could not be tested because large but highly variable catches on the outer-shelf in winter 1994 resulted in high heterogeneity of variances. Mean catch rates were 48.6 tow^{-1} in winter 1994 compared with 1.9 tow^{-1} in winter 1993, indicating considerable year-to-year variations in abundance

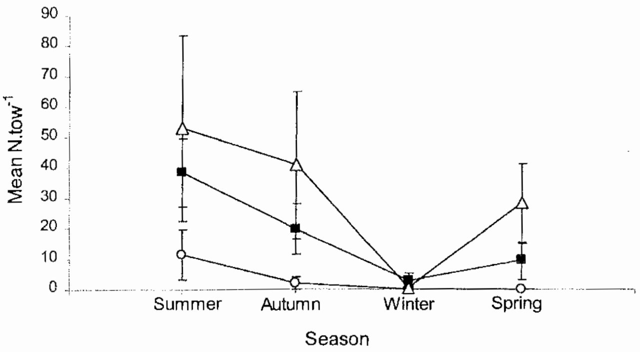


Fig. 2. Mean seasonal abundance (N tow^{-1}) of *Nemadactylus macropterus* collected from (○) inner-shelf (10–50 m), (■) mid-shelf (50–100 m) and (△) outer-shelf (100–200 m) strata on the east coast during 1993. Error bars, s.e.

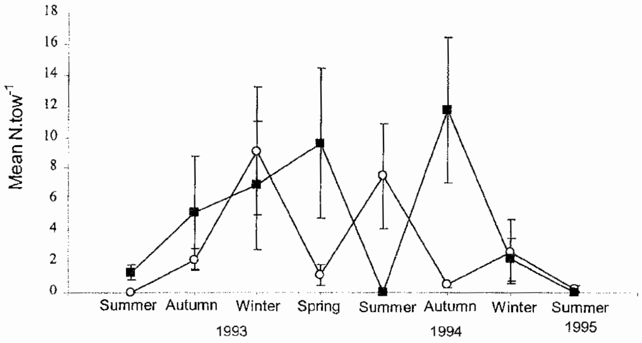


Fig. 4. Mean seasonal abundance (N tow^{-1}) of juvenile *Nemadactylus macropterus* collected from (○) inner-shelf (10–50 m) and (■) mid-shelf (50–100 m) strata in Storm Bay between summer 1993 and summer 1995. Error bars, s.e.

in winter. Although such differences may also result from patchy distribution, station density was higher in winter 1993, which would result in an increased chance of sampling a patch of *N. macropterus* in that year.

Abundances of mature *N. macropterus* on the shelf region of the east coast in the summers of 1993, 1994 and 1995 varied significantly only amongst depths ($P<0.001$) (Fig. 3). Post-hoc tests showed that abundances were significantly higher on the outer-shelf than on the mid-shelf, which in turn was significantly higher than on the inner-shelf (Ryans Q-test; $P<0.05$).

Abundances of juvenile *Nemadactylus macropterus* on the shelf of Storm Bay varied significantly amongst seasons ($P<0.05$), and there was also a significant season and depth interaction ($P<0.05$) (Fig. 4). Post-hoc tests indicated that, in terms of season, the major pattern was that on the inner-shelf, winter 1993 and summer 1994 were significantly higher than all other seasons (Ryans Q-test; $P<0.05$), whereas on the mid-shelf, autumn 1994 was significantly higher than all three summers, but not significantly different from all other seasons (Ryans Q-test; $P<0.01$). In terms of depths, abundances were significantly higher in winter 1993 than in all other seasons (Ryans Q-test; $P<0.05$).

The significance of the interannual variations in abundance of 0+ *N. macropterus* could not be analysed because patchy distribution of this age-class resulted in high heterogeneity of variances. However, variation in the means indicates that settlement of 0+ *N. macropterus* was highest on the east coast in 1993, highest in Storm Bay in 1994, and was extremely low in both shelf regions in 1995 (Fig. 5).

Size composition

Nemadactylus macropterus on the shelf of the east coast ranged from 8.5 to 45.5 cm, with the distribution consisting primarily of a single mode at 34 cm, with two considerably smaller modes at 9 and 15 cm (Fig. 6). The population was dominated by fish above the size at 50% maturity (25–27 cm) (Jordan 1998), making up ~90% of the population.

The size compositions of *N. macropterus* on the inner-

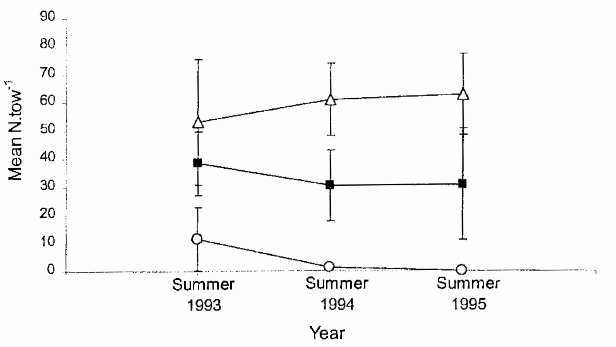


Fig. 3. Mean abundance (N tow^{-1}) of mature *Nemadactylus macropterus* collected from (○) inner-shelf (10–50 m), (■) mid-shelf (50–100 m) and (△) outer-shelf (100–200 m) strata on the east coast in summer 1993, 1994 and 1995. Error bars, s.e.

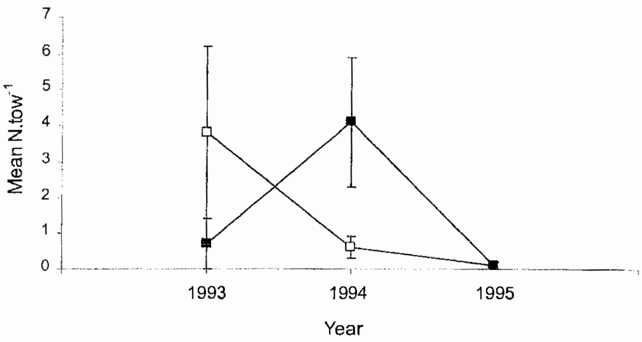


Fig. 5. Mean abundance (N tow^{-1}) of 0+ *Nemadactylus macropterus* collected from inner-shelf (10–50 m) and mid-shelf (50–100 m) strata combined during summer 1993, 1994 and 1995 on (□) the east coast and (■) Storm Bay. Error bars, s.e.

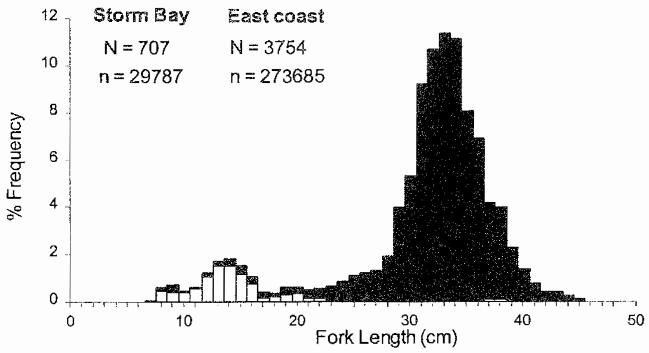


Fig. 6. Scaled length–frequency distribution of *Nemadactylus macropterus* collected on the shelf of (light bars) Storm Bay and (dark bars) the east coast between summer 1993 and summer 1995. N, measured sample size; n, scaled sample size.

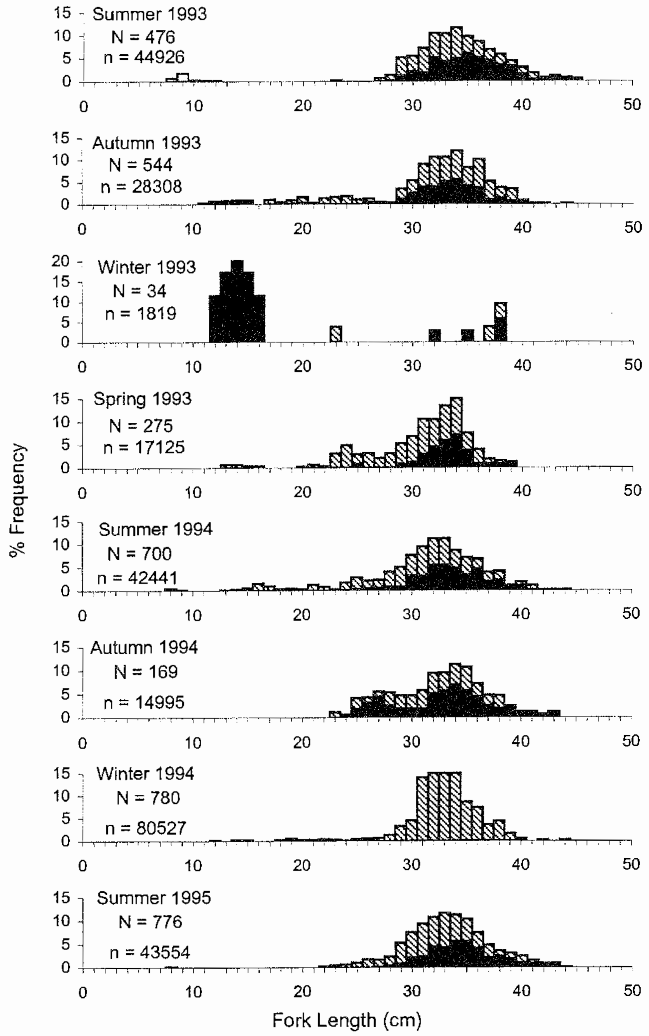


Fig. 7. Seasonal scaled length–frequency distribution of *Nemadactylus macropterus* collected on (light bars) inner-shelf, (dark bars) mid-shelf and (striped bars) outer-shelf strata of the east coast between summer 1993 and summer 1995. N, measured sample size; n, scaled sample size.

and mid-shelf regions of Storm Bay ranged from 6.6 to 45.1 cm, with the distribution dominated by a distinct mode at around 14 cm, with several smaller modes evident at 9 and 20 cm (Fig. 6). In contrast to the east coast, mature fish made up only around 6% of the population in Storm Bay. This to some extent reflects the lack of sampling in the outer-shelf stratum in Storm Bay, although very few mature fish were present on the mid-shelf compared with the same strata on the east coast.

Seasonal length–frequency distributions of *N. macropterus* on the east coast reveal distinct differences in the size compositions throughout the year and between years (Fig. 7). In 1993, mature fish dominated the population in all seasons except winter, although the proportion of fish >35 cm decreased from 47% in summer to 20% in spring, with evidence of an increased abundance of fish around 25 cm. The cohort with a mean length of 9.6 cm in summer 1993 represents 0+ fish from spawning the previous summer and autumn, this size-class progressing to 17.4 cm by summer 1994. In contrast, mature fish were present on the east coast in all seasons in 1994, and although there was no distinct seasonal change in the proportion of large fish, a higher proportion of fish between 20 and 30 cm was present in autumn. Size compositions in summer 1995 were normally distributed with a mean of 33.5 cm, which is consistent with those in previous summers.

Comparison of size compositions by depth indicates little difference in the size composition of *N. macropterus* on the mid- and outer-shelf of the east coast (Fig. 7). All size-classes were present in both strata, with no evidence of seasonal movement between strata, except for winter 1994 when fish were caught exclusively on the outer-shelf. *N. macropterus* were present on the inner-shelf only in summer in all three years and consisted exclusively of fish <12 cm.

Seasonal length–frequency distributions of *N. macropterus* in Storm Bay reveal the presence of significant numbers of mature fish only in summer and spring 1993 (Fig. 8). Most seasons were dominated by a cohort that first appeared in summer 1993 with a mean length of 8.4 cm, representing the 0+ age-class. This size-class was present again in summer 1994, although some settlement was apparent in spring 1993, suggesting that settlement occurs over an extended period. This is supported by the broad range of lengths of the 0+ age-class in summer, ranging from 6.6 to 11.1 cm. Given an arbitrary birthdate of 1 March, which corresponds to the mid-point of the spawning season in south-eastern Tasmania (Jordan 1998), the 0+ age-class in summer 1993 progressed into the 1+ age-class by autumn 1993, with a mean length of 11.8 cm. This size-class progressed to a mean length of 15.0 cm by spring 1993 and can be followed into the 2+ age-class in autumn 1994, with a mean length of 20.8 cm.

Comparison of size compositions by depth in Storm Bay indicates some size structuring of *N. macropterus* on the

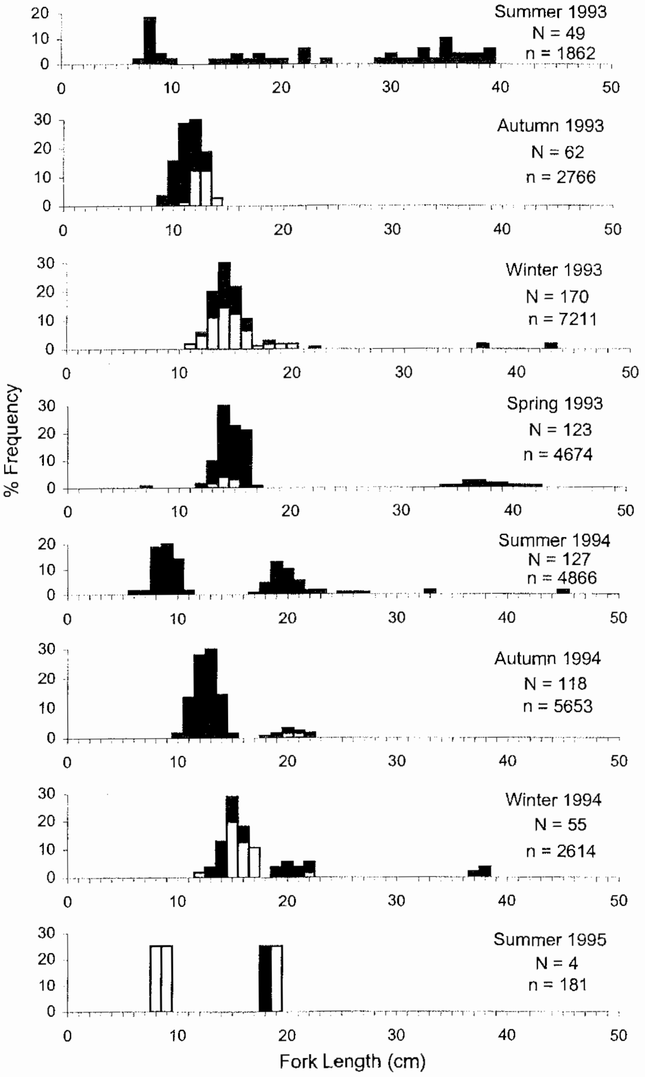


Fig. 8. Seasonal scaled length–frequency distribution of *Nemadactylus macropterus* collected on (light bars) inner-shelf and (dark bars) mid-shelf strata of Storm Bay between summer 1993 and 1995. N, measured sample size; n, scaled sample size.

inner- and mid-shelf, with mature fish restricted to the mid-shelf (Fig. 8). In contrast, juveniles were evenly distributed between the two strata, although in some seasons, fish were caught almost exclusively in a single stratum, such as summer 1993 when fish were restricted to the mid-shelf, and summer 1994 when 96% of fish were caught on the inner-shelf. This lack of depth preference is consistent across the 0+, 1+ and 2+ age-classes, with no indication of size- or age-structuring by depth of juveniles across the shelf of Storm Bay. This also indicates that there is little specific preference in the depth of initial settlement from the pelagic postlarval phase.

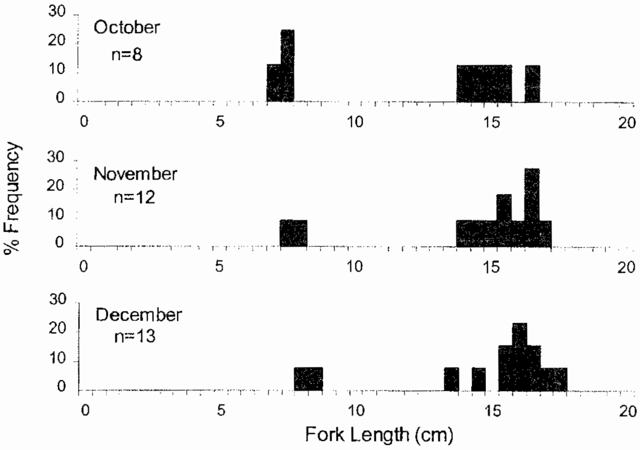


Fig. 9. Monthly length–frequency distribution of *Nemadactylus macropterus* collected on the inshore region of south-eastern Tasmania between October and December 1995. n, sample size.

Nearshore region

Very few *N. macropterus* were caught in nearshore waters despite extensive sampling of seagrass and unvegetated habitats with several gear types in three areas along the south and east coast (Jordan 1998). However, vulnerability of juvenile *N. macropterus* to beam trawls appears to be low during the day as all catches were made in targeted sampling at night conducted over the settlement period. Juvenile fish in shallow coastal waters have been observed schooling midwater during the day over subtidal reefs adjacent to unvegetated habitats (Last 1983). The length–frequency distributions of *N. macropterus* from nearshore regions of south-eastern Tasmania ranged from 7.4 to 17.5 cm, with the distribution dominated by two modes at around 7–8 cm and 15–16 cm (Fig. 9), which represent the 0+ and 1+ age-classes, respectively. Both-age classes were caught in unvegetated soft-mud habitats in depths of 3–12 m. Of significance is the lack of larger juvenile or adult *N. macropterus* in nearshore waters, despite the extensive use of small mesh gill-nets.

Discussion

The present study revealed considerable seasonal variations in the abundance of *N. macropterus* on the shelf of eastern Tasmania during 1993. Although abundances were significantly different only in winter, a trend of decreasing abundance from summer during autumn to a low in winter was apparent. The variations were primarily driven by the decrease in abundance of mature fish on the mid- and outer-shelf. In contrast, abundance of *N. macropterus* on the shelf of eastern Bass Strait is highest in autumn before decreasing to a low in spring and summer, the autumn peak being attributed to an influx of fish and changes in vulnerability due to spawning at that time (Wankowski and Moulton

1986). The contrasting trends in abundance between the two shelf areas suggest that there may be some movement of fish from eastern Tasmania into eastern Bass Strait during autumn. As spawning peaks in summer in eastern Tasmania (Jordan 1997) compared with autumn in eastern Bass Strait (Hobday and Wankowski 1987), and the change in abundance consists primarily of mature fish, such movements may be related to spawning. Migration of mature fish into discrete spawning grounds is reported in New Zealand (Annala 1987); however, no large scale movement of mature *N. macropterus* has been reported in Australian waters (Smith 1989).

Abundance of *N. macropterus* on the east coast during 1993 was consistently highest on the mid- and outer-shelf, reflecting the fact that both strata are dominated by mature fish. A comparison between all three summers also shows that abundance was consistently highest on the outer-shelf in this season, which is consistent for *N. macropterus* around Tasmania (Lyle and Ford 1993), and from commercial catches throughout the entire South East Fishery (Smith 1994). There was also evidence of interannual variations in the abundance of *N. macropterus* during winter on the east coast, with catch rates in 1994 considerable higher than those in 1993. The reasons for the peak in abundance in winter 1994 are unclear but appear to be unrelated to variations in secondary productivity because micronekton biomass was lower on the shelf of eastern Tasmania in winter 1994 than in 1993 (Young *et al.* 1996). This result suggests that further research is required on patterns of demersal productivity before the role of environmental factors in influencing CPUE in the commercial fishery can be separated from changes in stock abundance.

The size composition of mature *N. macropterus* in the present study is consistent with those from the commercial inshore trawl catch in Tasmania (mean 34.6 cm; range 25–47 cm) (Lyle and Lennon 1996). This is larger than *N. macropterus* in commercial catches from New South Wales and north-eastern Victoria, although such commercial size compositions vary considerably between years (Smith 1995). Smith (1994) suggested that the greater proportion of larger fish in eastern Tasmania than those from eastern Bass Strait reflects a lower level of exploitation in Tasmania. Alternatively, such differences could result from differences in growth, age composition or sex structure of the population.

There is clear evidence of size-structuring of the population of *N. macropterus* with depth, with the inner-shelf consisting exclusively of juveniles and the mid- and outer-shelf of juveniles and mature fish. Regional differences were also apparent, with very few mature fish present on the mid-shelf of Storm Bay compared with the east coast, indicating clear differences in the significance of the two shelf regions for mature *N. macropterus*. This is clearly reflected in the distribution of commercial trawl catches in the region, which is concentrated on the east coast (Lyle 1994). Such regional differences are also apparent in New Zealand where most nursery areas are spatially distinct from the mature population, with fish returning to their parental spawning grounds with the onset of maturity (Vooren 1975). Such variations are also evident over a broad scale in Australia, with juveniles absent from the shelf region of southern New South Wales, north-eastern Victoria and the Great Australian Bight, fish moving into these areas upon maturity at an age of ~3 years (Smith 1982, 1983). Given the significance of inner- and mid-shelf regions for juvenile *N. macropterus*, the large shelf area in these depths in south-eastern Tasmania relative to adjacent shelf waters suggests that this region is an important nursery area for the species. The size structuring by depth is consistent with many demersal species that also use inner- and mid-shelf waters in this region as a nursery area, including tiger flathead (*Neoplatycephalus richardsoni*), silver dory (*Cyttus australis*) and latchet (*Pterygotrigla polyommata*) (Jordan 1997).

There were no consistent seasonal variations in the abundance of juvenile *N. macropterus* in Storm Bay, with the trends in abundance on the inner-shelf reflecting the increased abundance of 1+ fish in winter 1993 and 0+ and 1+ fish in summer 1994. This, however, was not consistent between years as juvenile fish were mostly absent from the inner-shelf in summer 1993 and 1995, spring 1993 and autumn 1994. The presence of significant interactions between seasons and depths indicates considerable seasonal movement of 1+ and 2+ fish between strata in Storm Bay. Despite this, initial settlement of 0+ fish in Storm Bay in summer occurred exclusively into a single stratum in any year, with movement between strata apparent by autumn.

Recent settlement was indicated by the fact that all fish <8 cm were either post-larvae, or intermediate between post-larvae and juveniles. Post-larval *N. macropterus* are morphologically very different from juveniles and are characterized by a deep, thin, laterally compressed body with a sharply keeled belly and silvery appearance below the lateral line, often referred to as 'paperfish' (Vooren 1972; Bruce 1998). Close to the size at settlement, *N. macropterus* undergo metamorphosis from the pelagic post-larval phase into juveniles that are morphologically similar to adults. Settlement of *N. macropterus* in New Zealand waters also occurs prior to metamorphosis at around 6.3–7.0 cm (Vooren 1972).

Recruitment of pelagic post-larvae to shelf waters of Storm Bay and the east coast occurred over an extended period during spring and early summer (September–January) after an extended post-larval phase in offshore waters. In late autumn–early winter (May–June), *N. macropterus* larvae are found in surface waters up to 250 km offshore of eastern Tasmania (the limit of sampling), with larvae widely distributed offshore in water of subantarctic origin and East Australian Current (EAC) water, and within the broad convergence zone between the two (Bruce *et al.* 2001). The duration between spawning and settlement in Tasmania indicates that *N. macropterus* has a long larval duration of ~8–12 months, which is consistent with both the estimated age at settlement from microincrements of ~8–9 months old (Gauldie 1994) and period of retention of offshore Tasmanian waters of 8–12 months, indicated by the movement of surface drifters (Bruce *et al.* 2001). The extended settlement period in Tasmania is likely to be related to the prolonged spawning period in southern and eastern Tasmania (January–May) (Jordan 1998) and to short-term variations in the regional oceanography, with rapid advances and retreats of EAC water occurring during the settlement period (Harris *et al.* 1987).

There was little evidence of large differences in the timing of settlement of *N. macropterus*, despite evidence of variability in the oceanography and westerly wind stress in the study area during the summers of 1993, 1994 and 1995 (Young *et al.* 1996; Jordan 1998). The seasonal sampling, however, is likely to miss finer scale temporal patterns of recruitment resulting from variability in post-larval supply. If this supply is strongly influenced by physical transport processes then the short-term variations in westerly wind stress and oceanography that are common in the area are likely to result in short-term variations in recruitment.

The varying influence of water masses on Storm Bay and the east coast may also influence the spatial patterns of settlement, with the present data indicating reversals in the shelf regions with highest abundance of 0+ fish between 1993 and 1994, and a considerable decrease in the abundance in both regions in 1995. Similar interannual variability in the abundance of 0+ *N. macropterus* recruiting to individual nursery areas also occurs in New Zealand waters (Vooren 1975), with passive transport by mesoscale current systems hypothesized to influence the spatial patterns of settlement (Annala 1987). No such clear relationships existed in the present study between the abundance of 0+ fish and local hydrography, as recruitment peaked in Storm Bay in 1993, despite both shelf regions being dominated by subantarctic water during spring and summer in that year (Jordan 1998).

Although the role of passive transport in determining patterns of recruitment of *N. macropterus* is still to be examined, the large size at settlement (~7 cm) and lack of consistent onshore flow of surface waters during spring on the east coast suggest that active horizontal swimming plays a role in the movement of fish into the inner- and mid-shelf regions. The width of the shelf of southern and eastern Tasmania ranges from 20 Nm on the east coast to 40 Nm in Storm Bay. If larvae are retained within 100 Nm of the shelf edge, at an average swimming speed of two body lengths per second (Blaxter 1986), a 6 cm post-larva would take between 21 and 25 days to move onto the inner-shelf. Horizontal swimming has also been implicated in the onshore movement of pelagic juveniles (Larson *et al.* 1994; Hare and Cowen 1996), although such onshore transport still appears to be associated with hydrological features, such as internal waves (Shanks 1983; Kingsford and Choat 1986), warm core ring streamers (Hare and Cowen 1996) and Ekman transport (Shenker *et al.* 1993).

Spatial and temporal variations in abundance of juveniles may also reflect differences in post-settlement mortality, although factors such as shelter (Shulman and Ogden 1987), habitat complexity (Levin 1994) and physical disturbance (Stephens *et al.* 1994; Jenkins *et al.* 1997) are unlikely to be of significance for *N. macropterus* that recruit to unvegetated, deeper subtidal habitats. The lack of data on benthic productivity in shelf habitats precludes an assessment of food limitation as a major source of mortality. In addition, analysis of gut contents of demersal shelf species in the study areas found no evidence of significant predation of newly recruited *N. macropterus* (A. Jordan, unpublished), suggesting that variations in recruitment are primarily driven by post-larval supply.

Despite strong recruitment variability being demonstrated for *N. macropterus* from estimates of age-structure in New Zealand (Vooren 1977) and south-eastern Australia (Smith 1989), the role of environmental and biotic factors in recruitment success has not been closely examined. It is clear that to determine the mechanisms of onshore transport of post-larval *N. macropterus* and assess the influence of oceanography on recruitment strength, more detailed studies are needed on the hydrography of offshore and shelf waters at a range of spatial scales, particularly during spring and early summer, in addition to finer scale monitoring of temporal patterns of settlement and an examination of swimming abilities in post-larvae. In particular, the relationship between temporal patterns of settlement of *N. macropterus* and periodicity of westerly wind stress warrants further examination. Such studies would also provide a better understanding of the recruitment dynamics of several commercially important species in Tasmania that have an extended offshore larval distribution and show strong recruitment variations, including southern rock lobster (*Jasus edwardsii*), bastard trumpeter (*Latridopsis forsteri*), striped trumpeter (*Latris lineata*) and banded morwong (*Cheilodactylus spectabilis*) (Harris *et al.* 1988; Murphy and Lyle 1998).

Acknowledgments

Thanks to the captain and crew of FRV *Challenger* who provided great support during shelf surveys. Thanks also go to the many staff of the Marine Research Laboratories including David Mills, Graeme Ewing, Tristan Richards, Fiona Ewing and Ray Murphy who provided assistance at sea and in the laboratory. Thanks also to Jeremy Lyle and Robert White and two referees for providing comments on the manuscript.

References

Annala, J. H. (1987). The biology and fishery of tarakihi, *Nemadactylus macropterus*, in New Zealand waters. Fisheries Research Division Occasional Publication, New Zealand Ministry of Agriculture and Fisheries No. 51. 16 pp.

Blaxter, J. H. S. (1986). Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society* **115**, 98–114.

Bruce, B. D. (1998). Family: Cheilodactylidae. In 'The Larvae of Temperate Australian Fishes: a Laboratory Guide for Larval Fish Identification'. (Eds F. J. Neira, A. G. Miskiewicz and T. Trnski.) pp. 210–13. (University of Western Australia Press: Nedlands, WA.)

Bruce, B. D., Young, J. W., Evans, K., Sutton, C. A., and Furlani, D. M. (2001). The influence of mesoscale physical oceanographic processes on larval distribution and stock structure in jackass morwong (*Nemadactylus macropterus*, Cheilodactylidae). *ICES Journal of Marine Science*. (In press.)

Davis, T. L. O., and West, G. J. (1992). Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the north west shelf of Australia. *Fishery Bulletin (US)* **90**, 395–404.

Day, R. W., and Quinn, G. P. (1989). Comparison of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**, 433–63.

Gauldie, R. W. (1994). The morphological basis of fish age determination methods based on the otolith of *Nemadactylus macropterus*. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2341–62.

Graham, K. J., Liggins, G. W., and Wildforster, J. (1996). Kapala Cruise Report No. 115. (Fisheries Research Institute, NSW Fisheries: Australia.)

Hare, J. A., and Cowen, R. K. (1996). Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. *Limnology and Oceanography* **41**, 1264–80.

Harris, G. P., Nilsson, C., Clementson, L. A., and Thomas, D. (1987). The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. *Australian Journal of Marine and Freshwater Research* **38**, 569–90.

Harris, G. P., Davies, P., Nunez, M., and Meyers, G. (1988). Interannual variability in climate in Tasmania and its effect on freshwater and marine fisheries. *Nature* **333**, 754–7.

Hobday, D. K. and Wankowski, J. W. J. (1987). Jackass morwong *Nemadactylus macropterus*: Reproduction and fecundity in eastern Bass Strait, Australia. Department of Conservation Forests and Lands, Victoria. Marine Science Laboratories Internal Report No. 155. 17 pp.

Jenkins, G. P., Black, K. P., Wheatley, M. J., and Hatton, D. N. (1997). Temporal and spatial variability in recruitment of a temperate, seagrass-associated fish is largely determined by physical processes in the pre- and post-settlement phases. *Marine Ecology Progress Series* **148**, 23–35.

Jordan, A. R. (1997). Demersal trawl surveys of the continental shelf of southern and eastern Tasmania 1993–95. Technical Report of the Marine Laboratories Marine Research Division Tasmania No. 50, 148 pp.

Jordan, A. R. (1998). The life-history ecology of *Platycephalus bassensis* and *Nemadactylus macropterus*. PhD Thesis, University of Tasmania, Hobart, Australia.

Kingsford, M. J., and Choat, J. H. (1986). The influence of surface slicks on the distribution and movements of small fish. *Marine Biology* **91**, 161–71.

Larson, R. J., Lenarz, W. H., and Ralston, S. (1994). The distribution of pelagic juvenile rockfish of the genus *Sebastes* in the upwelling region off central California. *Californian Cooperative Oceanic Fisheries Investigation Report* **35**, 175–219.

Last, P. (1983). Aspects of the ecology and zoogeography of fishes from soft-bottom habitats of the Tasmanian shore zone. Ph.D. Thesis, University of Tasmania, Hobart, Australia.

Levin, P. S. (1994). Fine-scale temporal variation in recruitment of a temperate demersal fish; the importance of settlement versus post-settlement loss. *Oecologia* **9**, 124–33.

Lyle, J. M. (1994). Fishery Status Report: inshore trawl fishery. Department of Primary Industry and Fisheries, Marine Resources Division Internal Report No. 9. 75 pp.

Lyle, J. M. and Ford, W. B. (1993). Review of trawl research 1979–87, with summaries of biological information for the major trawl species. Technical Report of the Marine Laboratories Marine Research Division Tasmania No. 46. 169 pp.

Lyle, J. M., and Jordan, A. R. (1998). Tasmanian Scalefish Fishery Assessment — 1998. Fishery Assessment Report of the Tasmanian Aquaculture and Fisheries Institute. 98 pp.

Lyle, J. M., and Lennon, S. (1996). Size composition of Tasmanian scalefish landings derived from market sampling: 1978–93. Department of Primary Industry and Fisheries, Marine Resources Division Internal Report No. 25.

Martin, S. A., and Toothaker, L. E. (1989). PERITZ: a FORTRAN program for performing multiple comparisons of means using the Peritz Q method. *Behaviour Research Methods, Instruments and Computers* **21**, 465–72.

Murphy, R., and Lyle, J. M. (1998). Impact of gillnet fishing on inshore temperate reef fishes, with particular reference to banded morwong. Final Report to Fisheries Research and Development Corporation, Project No. 95/145.

Shanks, A. L. (1983). Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Marine Ecology Progress Series* **13**, 311–15.

Shenker, J. M., Maddox, E. D., Wishinski, E., Pearl, A., Thorrold, S. R., and Smith, N. (1993). Onshore transport of settlement stage Nassau grouper, *Epinephelus striatus*, and other fish in Exuma Sound, Bahamas. *Marine Ecology Progress Series* **98**, 31–43.

Shulman, M. J., and Ogden, J. C. (1987). What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Carribbean reef fish *Haemulon flavolineatum*. *Marine Ecology Progress Series* **39**, 233–42.

Smith, D. C. (1982). Age and growth of jackass morwong (*Nemadactylus macropterus* Bloch and Schneider) in eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **33**, 245–53.

Smith, D. C. (1983). Annual total mortality and population structure of jackass morwong (*Nemadactylus macropterus* Bloch and Schneider) in eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **33**, 253–60.

Smith, D. C. (1989). The fisheries biology of jackass morwong (*Nemadactylus macropterus* Bloch and Schneider) in south-eastern Australian waters. Ph.D. Thesis, University of New South Wales, Australia.

Smith, D. C. (1994). Jackass morwong. 'The South East Fishery: a scientific review with particular reference to quota management'. (Ed. R. D. J. Tilzey.) Bureau of Resource Sciences Bulletin.

Smith, D. C. (1995). Jackass morwong 1994, Stock Assessment Report, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Stephens, J. S., Morris, P. A., Zerba, K., and Love, M. (1994). Factors affecting fish diversity on a temperate reef: the assemblage of Palos Verdes Point, 1974–1981. *Environmental Biology of Fishes* **11**, 259–75.

Tilzey, R. D. J. (Ed.) (1999). The South East Fishery 1998. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Vooren, C. M. (1972). Postlarvae and juveniles of the tarakihi (Teleostei : Cheilodactylidae) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **6**, 602–18.

Vooren, C. M. (1975). Nursery grounds of tarakihi (Teleostei : Cheilodactylidae) around New Zealand. *New Zealand Journal of Marine and Freshwater Research* **9**, 121–58.

Vooren, C. M. (1977). Growth and mortality of tarakihi (Teleostei : Cheilodactylidae) in lightly exploited populations. *New Zealand Journal of Marine and Freshwater Research* **11**, 1–22.

Wankowski, J. W., and Moulton, P. L. (1986). Distribution, abundance and biomass estimates of commercially important demersal fish species in eastern Bass Strait, Australia. Department of Conservation Forests and Lands, Victoria. Marine Science Laboratories Internal Report No. 62.

Young, J. W., Bradford, R. W., Lamb, T. D., and Lyne, V. D. (1996). Biomass of zooplankton and micronekton in the southern bluefin tuna fishing grounds off eastern Tasmania, Australia. *Marine Ecology Progress Series* **138**, 1–14.

Manuscript received 5 November 1999; revised and accepted 24 February 2000

Mar. Freshwater Res., 2001, **52**, 671–81

Approach and process for stock assessment in the South East Fishery, Australia: a perspective

David C. Smith[A], *Anthony D. M. Smith*[B] *and André E. Punt*[B]

[A]Marine and Freshwater Resources Institute, Department of Natural Resources and Environment, PO Box 114, Queenscliff, Vic. 3225, Australia
[B]CSIRO Division of Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia

Abstract. The stock assessment process in the South East Fishery involves scientists, industry, fishery managers, economists and non-government organizations. A comparison with such processes in other countries, where stakeholder involvement ranges from government scientists only to involvement of scientists, industry and conservation non-government organizations, suggests that Australia is the only country in which fishery managers are active and integral stock-assessment participants. In Australia, as in several other countries, the form of advice is comparative (consequences of alternative decisions) rather than prescriptive. Although all approaches have advantages and disadvantages, the South East Fishery process has advantages that appear to clearly outweigh the disadvantages. The advantages include better communication among interest groups, improved ownership of and hence support for outcomes and better interactions among groups. The disadvantages include the cost of the process, lack of consistency among assessments, vulnerability of scientists and the frustrations of industry.

Abbreviations

AFFA	Agriculture, Fisheries and Forestry–Australia
AFMA	Australian Fisheries Management Authority
SEF	South East Fishery
SEFAG	South East Fishery Assessment Group
SENTMAC	South East Non-trawl Management Advisory Committee
SETF	South East Trawl Fishery
SETMAC	South East Trawl Management Advisory Committee

Introduction

The South East Fishery (SEF) is a multi-species, multi-method fishery operating in south eastern Australia in depths of 50–1200 m. Since 1992, the fishery has been managed primarily through Individual Transferable Quotas (ITQs) for 16 species or species groups that contribute ~80% of the total catch (Tilzey 1998). The life histories of these species vary enormously, from short-lived species such as school whiting (*Sillago flindersi*, maximum age <10 years) living in shallow coastal waters (<100 m) to extremely long-lived species such as orange roughy (*Hoplostethus antlanticus*, maximum age >100 years) living in depths of >1000 m. Total Allowable Catches (TACs) are set for these species each year. Day-to-day management of the fishery is the responsibility of the Board of the Australian Fisheries Management Authority (AFMA) while the development of fisheries policy is the responsibility of a federal government department (Agriculture, Fisheries and Forestry-Australia, AFFA)

There is ample literature on the origins and history of Australia's oldest trawl fishery (Fairbridge 1948; Houston 1955; Graham *et al.* 1982; Smith 1991; Tilzey 1994; Grieve and Richardson 2001; Tilzey and Rowling 2001). Commencing in 1915, the fishery has undergone several overlapping phases that have seen its extent and complexity increase considerably. The fishery was initially known as the East Coast Trawl and Danish Seine Fishery and then the South East Trawl Fishery (SETF). Until the 1970s, the fishery was based on continental-shelf resources, primarily off New South Wales and eastern Victoria. During the 1970s, the fishery expanded to western Victoria, South Australia, and Tasmania, and to waters deeper than 200 m. The fishery further expanded to include mid-slope waters down to 1200 m following the discovery of orange roughy aggregations during the 1980s.

Late in 1992, AFMA changed the name of the fishery from the South East Trawl Fishery to the South East Fishery, reflecting the fact that several quota species were also taken by non-trawl methods (Tilzey 1994). Consequently, the SEF comprises two sectors, trawl and non-trawl, each with its own management advisory committee: the South East Trawl Management Advisory Committee, SETMAC, and the South East Non-trawl Management Advisory Committee, SENTMAC.

10.1071/MF00150 1323-1650/01/040671

Although aspects of the South East Fishery have been studied for a long time (e.g. Colefax 1938; Fairbridge 1951), it is only in recent years that a coordinated and systematic approach has been taken to quantitative stock assessment. Tilzey and Rowling (2001) describe in detail the history of research and monitoring in the SEF. The process by which stock assessments are undertaken and the resulting advice is given to management agencies has changed considerably in recent years. Broadly, there have been three periods, generally following the development of the fishery and changes to its management. Prior to the mid 1970s, studies were limited to a few key species (Colefax 1938; Fairbridge 1951, 1952; Houston 1955; Han 1964), summaries of the fishery, and port monitoring of the length frequency distributions of key species, particularly tiger flathead *Neoplatycephalus richardsoni*, jackass morwong *Nemadactylus macropterus* and redfish *Centroberyx affinis* (Blackburn 1978). As the fishery expanded during the 1970s and 1980s there was a large increase in research and monitoring by State agencies in NSW, Tasmania, Victoria and by federal agencies such as the Australian Fisheries Service and CSIRO (table 1 in Knuckey *et al.* 2000). For example, four agencies were involved in independent studies of blue grenadier *Macruronus novaezelandiae.*

The Demersal and Pelagic Fish Research Group, formed in 1973 as a forum for review and coordination of fisheries research conducted in south-eastern Australian, played an increasing role in the SEF, and by the mid 1980s was providing advice to the Australian Fisheries Service on the status of SEF fish stocks (Ross and Smith 1997; Tilzey 1998). The group comprised government scientists only. It was not considered appropriate for managers, industry or industry scientists to be part of the discussions. The group, in the absence of other arrangements, performed a useful function and this was acknowledged by the inclusion of the Chair of the group as a member of SETMAC.

A major development in the assessment of the fishery was the establishment of the Government/Industry Technical Liaison Committee in 1989 to coordinate research on orange roughy (Ross and Smith 1997). This was the first committee in south-eastern Australia that provided a forum for industry, scientists and managers to address scientific issues and research and monitoring requirements. Most participants believed it was effective and successful.

In 1993, AFMA formed the South East Fishery Assessment Group (SEFAG), which took over responsibility for annual assessments and the provision of scientific advice for TAC setting. Following AFMA's partnership approach (Smith *et al.* 1999), there is broad representation from industry, management and science on SEFAG.

In this paper we describe the processes and approach currently adopted for stock assessment in the South East Fishery, compare it with stock-assessment processes in other countries, and discuss its strengths and weaknesses.

The current SEF assessment process

Overview

The relationships among the current assessment and management committees in the SEF are shown schematically in Fig. 1. As with most fisheries under federal aegis, the SEF has a fishery assessment group (SEFAG) and a Research Sub-committee. The roles of these two committees are quite different although they liaise closely and there is broad overlap in membership. Generic terms of reference and functions are shown in Table 1. Primarily, SEFAG undertakes annual assessments on the status of the fishery and individual species and provides advice to the SEF TAC Sub-committee and to AFMA on the scientific basis for setting TACs. The TAC Sub-committee is a sub-committee of SETMAC and SENTMAC (Fig. 1) that is responsible for recommending TACs to the MACs for the following year. The MACs in turn provide advice to the AFMA Board, which makes the final decision regarding TACs. The SEFAG report is also available to the AFMA Board, as is advice from AFMA managers. The Research Sub-committee's primary role is to identify and set research priorities, and to evaluate research proposals. It is also responsible for the fishery's Strategic Research Plan. In this paper we are primarily concerned with the activities of SEFAG.

Current SEFAG membership includes a Chair (scientist), two industry representatives from each sector (trawl and non-trawl), an industry scientist, five Government scientific members (one each from NSW, Victoria, Tasmania and one each from the federal science agencies the Bureau of Rural Sciences and CSIRO), an economist from the Australian Bureau of Agricultural and Resource Economics, and an AFMA manager and secretary. SEFAG also includes a member from an environmental non-government organization (NGO). In addition, the scientific members of SETMAC and SENTMAC are also expected to attend SEFAG meetings. Other persons may be co-opted as required on to the group to participate in discussions or may be contracted to conduct or write individual species assessments.

Although industry representatives are members of SEFAG, a series of port meetings and occasional species-specific workshops are also held each year to ensure the widest possible input of industry views and experience into the process and to disseminate assessment results to a broad audience.

The activities of SEFAG have evolved since its establishment in 1993 and the changes are worth briefly reviewing. SEFAG prepared a Fishery Assessment Report in 1993 providing an overall assessment of the fishery and a compilation of stock-assessment summaries for each quota species (Staples *et al.* 1994). In 1994, a series of working groups and a SEFAG plenary reviewed species-specific

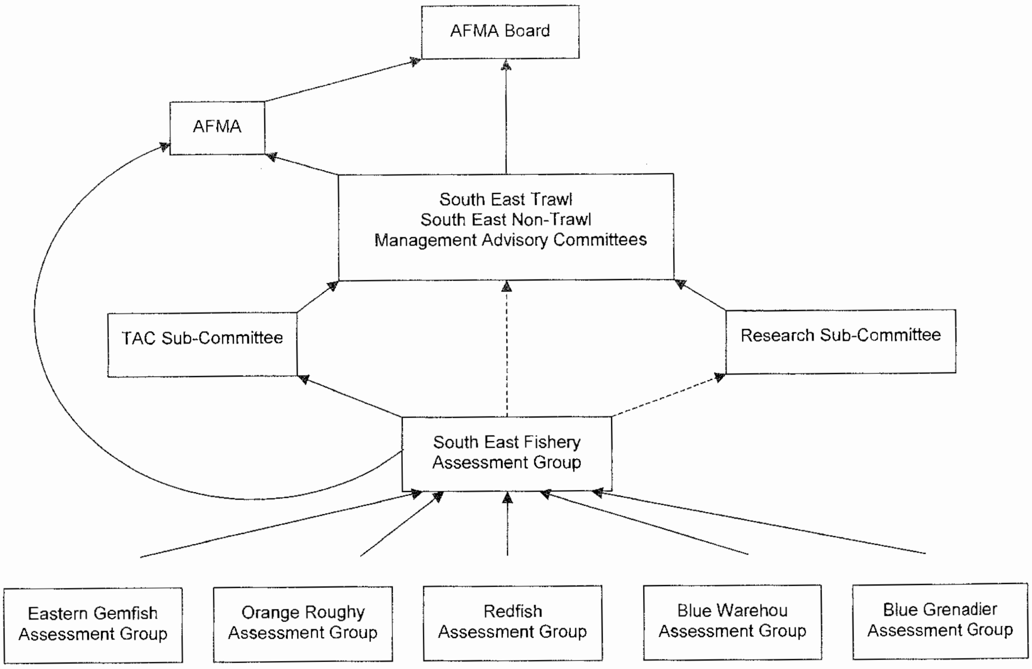


Fig. 1. Reporting arrangements and committee structure for the South East Fishery.

Table 1. Terms of reference and functions for AFMA Assessment Groups and the Research Subcommittees (B. Wallner, AFMA, personal communication)

MAC, Management Advisory Committee; FAG, Fishery Assessment Group; ARC, AFMA Research Committee; ComFRAB, Commonwealth Fisheries Research Advisory Board

Fishery Assesment Groups	Research Subcommittee
Terms of reference	
(1) Provide a forum for ongoing expert analysis, assessment, and reporting on the status of a commercial fishery, including target stocks, health of the marine environment supporting those stocks, and the economic efficiency with which those stocks are fished. *(2)* Strive to improve and refine assessment methods. *(3)* Undertake evaluations or analyses of harvest strategies or TAC settings, including advice on confidence limits or risk levels associated with particular management strategies. *(4)* Develop, test, refine and recommend sustainability indicators for the fishery. *(5)* Provide regular advice and recommendations to the ARC on issues consistent with FAG functions. *(6)* Liaise with other researchers, experts and key industry members. *(7)* Maintain awareness of current issues by promoting close links with MAC, AFMA and other FAGs.	*(1)* Identify and document fishery research gaps, needs and priorities. *(2)* Provide a forum for expert consideration of scientific issues referred by a MAC. *(3)* Provide a forum for detailed consideration of scientific issues raised by fishery stakeholders. *(4)* Develop and update a strategic research plan for the fishery and initiate research proposals in line with the strategic plan. *(5)* Provide advice to the MAC on matters consistent with MAC subcommittee functions. *(6)* Provide to the ARC/COMFRAB ranked evaluations for research proposals on an annual basis, and review reports and outcomes from completed projects. *(7)* Consult with the FAG to ensure that research priorities reflect assessment needs.
Functions	
(1) Fishery assessment and reporting (includes monitoring fishery trends, stock assessment, economic assessment and environmental assessment) *(2)* Identifying information needs and deficiencies for fishery assessments *(3)* Contributing to MAC identification of research gaps and needs *(4)* Advising MAC on biological, ecological and economic implications from stock assessments *(5)* Evaluating alternative harvest strategies for effects on stocks *(6)* Evaluating risks from alternative TAC settings *(7)* Developing sustainability indicators *(8)* Peer reviewing alternative independent assessments	*(1)* Identifying research gaps and needs (in consultation with the FAG) *(2)* Setting research priorities *(3)* Soliciting research proposals *(4)* Ranking proposals for ARC/COMFRAB *(5)* Evaluating research project reports *(6)* Developing and updating the fishery 5-year strategic research plan *(7)* Advising MAC on research issues as requested

Stock Assessment Reports produced by authors from a range of State and Commonwealth agencies. The 1993 Fishery Assessment Report was updated to reflect the outcomes of this process (Staples and Tilzey 1995). The Fishery Assessment Report has been updated each year since (Chesson 1996, 1997; Tilzey 1998, 1999; Smith and Wayte 2000, 2001) and this is now required by AFMA.

Up to 1996, SEFAG dealt with the assessment of individual species through working groups and workshops. However, disagreement about the assessment for eastern gemfish led during 1996 to the establishment of the Eastern Gemfish Assessment Group. This group, comprising scientists, industry (gemfish fishers), managers and an NGO representative, has met three times a year since 1996. One of its primary achievements was the establishment of an annual gemfish trawl survey and monitoring programme (Smith *et al.* 1999). It also invested considerable time and effort in improvements to the quantitative assessment (Smith and Punt 1999) and to evaluation of a species-specific harvest strategy (Punt and Smith 2000). Smith *et al* (1999) review some of the perceived successes and problems of this group.

Based on the success of EGAG, four more assessment groups were formed during 1997 and 1998: for blue grenadier, orange roughy, blue warehou and redfish. Thus, at the time of writing SEFAG has five species assessment groups covering six species (spotted warehou is now covered by the blue warehou assessment group; Fig. 1, Table 2). Assessment of other species continues to be dealt with through workshops or working groups or, for some minor species, simply through update and review of recent trends in logbook and catch-sampling data.

The primary role of each species assessment group is to assess the stock or species in relation to its particular management objectives, describe the management implications, and identify the research and monitoring necessary to improve the assessment. SEFAG and its species assessment groups do not make specific recommendations regarding management or future TACs, but instead describe the implications of alternative harvest strategies and, in a risk framework, the probabilities of meeting certain performance outcomes (generally in relation to biological reference points). Some assessment groups have also provided suggestions for quantitative management objectives, but these have to be endorsed by the MACs and ultimately by the AFMA Board.

SEFAG undertakes an annual review of all species reports, and submits the draft fishery assessment report to AFMA and the SEF TAC Sub-committee. The Chair of SEFAG also attends the TAC Sub-committee meeting as an advisor, providing brief summaries to assist the committee with its deliberations, and clarifying technical issues that arise. The MACs discuss the recommendations from the TAC Sub-committee, with the final decision on TACs being the responsibility of the AFMA Board.

Since its inception, SEFAG has overseen a significant increase in the number of quantitative stock assessments for SEF species. At its inception in 1993 there were recent quantitative assessments for only orange roughy and eastern gemfish. By 2000, there were regular or recent quantitative assessments for eight species (Table 2).

Monitoring and data collection

The increase in the number of quantitative assessments is partially attributable to improved data collection. Since late 1985, all fishers participating in the trawl fishery are required to complete a per-shot logbook, which has provided comprehensive catch-and-effort data for the first time. A logbook was also introduced into the non-trawl sector in 1997. Catch-and-effort data provide the main source for indices of abundance for individual species. Fishery-independent abundance indices that can be used for assessment purposes are available only for orange roughy and blue grenadier, but in both cases catch-rate data are also used. The eastern gemfish trawl survey is an attempt to replicate historical fishing patterns, and is not a random survey.

In addition to logbook data, landings information from the quota monitoring system is also used in assessments. Economic data based on annual surveys by the Australian Bureau of Resource Economics are available, but these are not used in quantitative stock assessments at present. The collection of age–length keys for SEF species was sporadic and in some cases duplicated across State agencies until the establishment of the Central Ageing Facility in 1991 (Morison *et al.* 1998). However, for the major species there are now sufficient age-composition data (Table 2) to enable the 'routine' use of catch-at-age data in quantitative assessments.

The introduction of the Scientific Monitoring Programme in 1995 and the Integrated Scientific Monitoring Programme (Smith *et al.* 1997; Knuckey *et al.* 2000) in 1997 has seen implementation of statistically rigorous port-based and at-sea monitoring in the SEF. The two programmes replaced the generally uncoordinated activities of the State and federal agencies. An important component of the integrated programme has been the collection of information on discards of non-commercial species as well as of quota and other commercial species; these data were not previously collected. Discard data have proved very important for several SEF assessments (e.g. Punt 1999; Punt *et al.* 2001*b*).

Funding sources

The assessment process, data collection and research are funded from several sources.

- The AFMA Research Fund. Monies amounting to slightly more than $A1 million annually are provided by the federal government to support AFMA's stock-assessment process

Table 2. Status of assessments and data availability for SEF species

'+' in the 'length' or 'age' column indicates that length–frequency and age–length keys have been collected regularly since 1991/92 (for some species, size and age data were collected before 1991/92, but it was from this year that consistent sampling was undertaken across the fishery). '*' in the 'age' column indicates that only occasional 'snapshots' have been taken of the catch age-composition

Species	Scientific name	Time series		Assessment group	Quantitative assessment
		Length	Age		
Blue-eye trevalla	*Hyperoglyphe antarctica*	+	+	–	–
Blue grenadier	*Macruronus novaezelandiae*	+	+	+	+
Blue warehou	*Seriolella brama*	+	+	+	+
Flathead	*Neoplatycephalus richardsoni*	+	+	–	–
Gemfish, eastern	*Rexea solandri* (eastern stock)	+	+	+	+
Gemfish, western	*Rexea solandri* (western stock)	+	*	–	–
Jackass morwong	*Nemadactylus macropterus*	+	+	–	–
John dory	*Zeus faber*	+	*	–	–
Ling	*Genypterus blacodes*	+	+	–	+
Mirror dory	*Zenopsis nebulosus*	+	*	–	–
Ocean perch	*Helicolenus* sp.	+	*	–	–
Orange roughy	*Hoplostethus atlanticus*	+	+	+	+
Redfish	*Centroberyx affinis*	+	+	+	+
Royal red prawn	*Haliporoides sibogae*	+	–	–	–
School whiting	*Sillago flindersi*	+	+	–	+
Silver trevally	*Pseudocaranx dentex*	+	*	–	–
Spotted warehou	*Seriolella punctata*	+	+	+	+

and some other research activities identified as priorities by the AFMA Research Committee. For the SEF, this fund supports the meeting and reporting costs of SEFAG and the other SEF assessment groups (currently ~$A360 000 per year). It also contributes to small management-related research projects.

- The Fisheries Resources Research Fund. This fund is administered by AFFA, and, for the SEF, currently supports the economic surveys by the Australian Bureau of Agricultural and Resource Economics and some of the data analyses undertaken by the Bureau of Rural Sciences.
- The Fisheries Research and Development Corporation. The corporation funds ~$A500 000-worth of research in the SEF each year. Unlike the two funds listed above, it will not fund 'routine' stock assessment or data collection, although it has been an important source of support for the development and application of quantitative methods for SEF stock assessment, including evaluation of harvest strategies. 75% of the monies are derived from the federal government and 25% from industry based on 1% of the gross value of production of the fishery.
- The Fishing Industry currently funds 80% of the cost of the Integrated Scientific Monitoring Programme and 100% of ongoing cost of ageing of SEF species. Industry also occasionally funds small individual research projects, and contributes important 'in kind' support for many research projects.

In addition to the above, various research agencies, such as CSIRO, allocate core funds to research and assessment in the SEF.

Comparison with other approaches and processes

New Zealand

The stock-assessment process in Australia is most similar to that in New Zealand. The New Zealand stock-assessment process is administered and run by the Ministry of Fisheries (MFish). All the assessment work is conducted by working groups, which are held throughout the year but primarily in February and March. Some working groups provide assessment advice for specific species (such as blue grenadier, rock lobster and snapper) whereas other working groups consider a number of species (Annala *et al.* 1999). Working groups are open to all interested parties, and participants include scientists (primarily from industry and government), industry representatives (including fishers), (occasionally) members of conservation groups, and representatives from the Treaty of Waitangi Fisheries Commission and other Maori iwi groups. The managers (MFish staff) do not participate as actively in the assessment groups as do those in Australia, although they oversee the process, use the outcomes to formulate policy advice, and occasionally chair meetings. Responsibility for conducting the technical details of the assessment and the associated data gathering (including biomass surveys, catch sampling, ageing and other research projects) are contracted out by MFish. To date, most fisheries research has been conducted by scientists from NIWA (National Institute of Water and Atmospheric Research), these being mainly former government scientists.

Like the situation in Australia, working groups do not provide management recommendations, but instead focus on providing scientific advice on yields and stock status, including determining the trade-offs achieved by alternative management actions. Uncertainty is emphasized and often several alternative models are examined. The outcomes for the contentious assessments are reviewed during a week-long stock-assessment plenary, which is a public meeting run by MFish. Unlike the situation for federally controlled fisheries in Australia, management decisions such as the setting of TACs are made by the Minister of Fisheries. The Minister's decision is based on advice from policy advisors in the Ministry of Fisheries who in turn base their advice on the outcomes from the assessment process together with relevant considerations from the Fisheries Act, and economic and social needs.

South Africa

The Minister of Environmental Affairs and Tourism is the decision-maker in South Africa. The Minister is advised by (but is not obliged to accept the advice of) the Consultative Advisory Forum. This forum consists of a wide range of stakeholders (such as scientists, industry, labour) and has a role roughly similar to that of the AFMA Board, although it is still only advisory. The assessment process in South Africa starts at a working-group level. Working groups are based around species or groups of species. Membership is restricted primarily to government scientists (and consultants paid by the government) although, recently, industry-funded scientists and industry observers have been attending some working-group meetings. Working groups generally consider the trade-offs among management actions but also indicate a preference among the alternatives. Management procedures (e.g. Butterworth *et al.* 1997) have been adopted for several species in South Africa. Management procedures comprise formally adopted rules for determining management arrangements (such as TACs) that include specifications for the data, and assessment models that will be used, together with the catch-control rule that is applied to the data or assessment to set the TAC. For species for which a management procedure is in place, the deliberations of the working group generally merely involve confirmation that the management procedure has been applied correctly. The report of each working group is sent to (and can be changed by) the Director of Marine and Coastal Management before being sent to the Consultative Advisory Forum. Scientists and representatives of industry discuss issues of relevance to the fishery (including assessments) at the Industry Sea Fisheries Forum.

The European Union

The decisions regarding management actions for fish stocks distributed exclusively in the waters of the European Union are made by a Council of Ministers (of Fisheries). The proposals on which the decisions are based are provided by the European Commission. These proposals are in turn based on the report of the ACFM (Advisory Committee on Fisheries Management) and of the Scientific, Technical, and Economic Committee on Fisheries, an in-house body of the European Commission that reviews ACFM advice and may endorse it or modify it in light of economic or other considerations. ACFM is a committee of the International Council for the Exploration of the Sea (ICES). ICES is a scientific body and the ICES assessment process is very different from that in Australia. Assessments are conducted by groups of scientists from ICES member countries. There is no industry or management participation in assessment groups, and it has been commented (Corten 1996) that 'the average fisheries biologist, working in one of the ICES working groups, will never meet any of the managers that are taking the decisions'. Although recommendations for the allowable catch for each species were made in the past by ACFM, this is no longer the case and, instead, ACFM indicates whether the stock is inside or outside what it considers to be safe biological limits, in terms of biomass and of fishing mortality rate. These biological limits take into account stock–recruit considerations, assessment uncertainty and occasionally also yield-per-recruit considerations.

For other European areas, management actions may be agreed within other regional organizations (e.g. the International Baltic Sea Fisheries Council, and the North-East Atlantic Fisheries Council) or directly by bilateral or multilateral agreements between the coastal states concerned, arrived at in a series of annual meetings. These negotiations usually take as their starting point the ACFM advice, although the extent to which the result of negotiations conforms to the advice is variable.

West Coast, USA

The management of commercial and recreational fisheries in USA waters of the 3–100 nmile zone is conducted through a set of eight Management Councils. The fisheries off the States of Washington, Oregon and California are managed by the Pacific Fishery Management Council. Assessments for groundfish species off the west coast are conducted by a stock-assessment team, which usually consists of a small group of government scientists. Some of the assessments are then presented to and reviewed by a stock-assessment review panel, which consists of government scientists (both local and from elsewhere in the USA) and outside scientists. There is iteration between the panel and the assessment team, and the final assessment may differ substantially from the initial draft. At no stage of this process are representatives of industry (or their scientists) involved (unless specially invited). The results of the assessment are reviewed by a Groundfish Management

Team, which consists of Federal and State scientists. On the basis of the assessment report, this team develops a catch projection document, which is reviewed by a Scientific and Statistical Committee (scientists) and a Groundfish Advisory Panel (industry). The Council process also includes public participation in the development of recommendations.

Atlantic Canada

The ultimate decision-maker in Canada is the Minister of Fisheries and Oceans. The process for providing advice differs among regions of Canada. Except in Atlantic Canada, the Minister is advised by the Fisheries Management Branch of the Department of Fisheries and Oceans, which holds consultations with industry regarding management actions. In contrast, in Atlantic Canada, the Minister is advised by the Fisheries Resource Conservation Council. The information supplied to the council is developed through a Regional Advisory Process. Stock-assessment work is conducted primarily (but not exclusively) by government scientists. Stock-assessment reports for Atlantic groundfish stocks do not provide recommendations but instead outline the trade-offs associated with different management actions. A review meeting evaluates the stock-assessment report and any associated documents (survey summaries, etc.). Participants in the review meeting include local Department of Fisheries and Oceans staff and invited members (e.g. members of industry, academics and scientists from other countries or parts of Canada). The review meeting makes suggestions for modifications to the assessment, additional diagnostic statistics and the like. The outcome of the review meeting, which consists of a scientific report and a stock-assessment summary, need not be a consensus document.

Summary of key differences

The AFMA assessment process, which is similar to that used in other Australian jurisdictions, is more open than those reviewed above. The New Zealand assessment process is the most similar, but its fishery managers do not participate so actively as those who participate in AFMA assessment groups. Unlike agencies in Canada, the European Union, South Africa and the USA, the Australian agency (AFMA) does not employ assessment staff but rather ‘contracts out’ assessment work — but, in contrast to New Zealand, several research agencies participate in assessment groups. Although the AFMA Board is appointed by the Australian Minister of Fisheries, this Minister has relatively little influence on day-to-day management decisions, including the setting of TACs for the SEF quota species. This differs markedly from the management approaches in Canada, New Zealand, South Africa, and Europe where elected politicians are the ultimate decisions makers and may play a very active role in selecting, for example, TACs. Assessment groups in the bulk of the countries reviewed and in Australia do not provide recommendations for management actions. However, the assessment groups in the US and to some extent South Africa make suggestions for management actions, including TACs.

Discussion

In just over 10 years, the process and approach by which stock assessment is undertaken in the South East Fishery has undergone profound change. It has moved from a forum of scientists only (similar to that still in operation in the European Union) to a process in which all significant stakeholders are involved. There has also been a notable improvement in the coordination of research, monitoring and assessment activities. These changes reflect the more widespread changes that have occurred in fisheries management in Australia over the past decade. AFMA was deliberately set up to be at arm’s length from Government, and with a strong commitment to a broad partnership approach to management (Smith *et al.* 1999). Similar levels of stakeholder participation occur in all AFMA-managed fisheries, including those managed under input controls.

The number of quantitative stock assessments has increased markedly during the 1990s, partly as a result of increased demands for scientific advice and input to the TAC-setting process and improved data collection mechanisms, but also because of an improved assessment process. Key features of recent assessments are that uncertainty (model as well as data) is dealt with explicitly, a wide range of sensitivity tests are conducted, results are provided in a risk-assessment framework, and are presented as the consequences of alternative management actions rather than as recommendations for specific management actions. By contrast, most of the stock assessments conducted before the late 1980s were based on deterministic models and the resultant management advice tended to be prescriptive.

Although all approaches have advantages and disadvantages, we contend that the process currently used in the SEF has advantages that clearly outweigh the disadvantages. Smith *et al* (1999) discuss the roles of the various players in the stock-assessment process in the context of facilitating evaluation and implementation of harvest strategies. They also outline some of the advantages and disadvantages of the AFMA partnership model for the stock-assessment process. The remainder of this discussion builds on that analysis, focusing on advantages of the process (better communication among interest groups, improved ownership of and hence support for outcomes) as well as some of the disadvantages (costs of the process, lack of consistency between assessments, vulnerability of scientists and frustrations of industry).

Although difficult to quantify, the interaction among participants is one of the major advantages of the process. It assists with communication and usually engenders a degree of trust and mutual respect when what are often conflicting parties are dealing with difficult issues. The importance of good communication cannot be over-stated. Often in the past, each interest group was effectively using a different language. Industry representatives did not understand and did not trust the technical aspects of assessments; they often could not (and this is still an issue) reconcile their own at-sea observations with the 'averaged' and longer-term stock assessments because there is a mismatch between the spatial and temporal scales used in assessment and fishers' own observations. By participating in the assessment process, stakeholder groups, particularly industry and managers, gain a conceptual understanding of stock assessment and modelling. The importance of communication goes both ways, of course. Industry can assist with interpretation of trends in the various data sets and clarify anomalies or what appear to be measurement or observation errors. This is particularly useful in fisheries like the SEF, where modellers and fisheries biologists rarely work in the field directly with industry. They can also identify some of the hypotheses that eventually form part of the assessment. The role of industry scientists has been important to the SEFAG process. They assist in communicating industry's views (e.g. Prince *et al.* 1999) and, conversely, in explaining the assessment outputs and their implications to the industry.

It seems surprising that fishery managers in countries outside Australia are rarely directly involved in the stock-assessment process. It should be important for managers to have a thorough understanding of the assessment, the key uncertainties and areas of contention because they have to implement the decisions that are based on the assessment. The involvement of managers in the assessment process has also proved useful during the selection of operational management objectives, performance measures and decision rules. These are clearly the responsibility of resource managers and the relevant management advisory committees and management agencies, and not of the scientists. However, in practice, developing them is an iterative process that interacts strongly with the scientific elements of the stock-assessment process. The quality of the assessment is often a key driver in their establishment. Certainly in SEFAG there has been frequent and on-going debate among participants about the choice and suitability of alternative performance measures that has seen an evolution towards more appropriate choices.

Conservation NGOs are represented on SEFAG, the SEF Research Sub-committee and the MACs but not on all single-species groups. Industry initially mistrusted the involvement of these representatives. However, given the increasing emphasis on broader ecological aspects in Australian fisheries, and increasing community concerns regarding the effects of fishing on the ecosystem, their input has been beneficial in assisting industry to deal with these issues and in broadening the focus of scientists. Thus, their involvement is important, in terms not just of perception, but also of outcome and focus.

'Ownership' of assessment outcomes is crucial. Often in the past scientists have worked, independently from both industry and managers, only to have their results criticized when they were presented, after, say, a three-year research project, to an often sceptical and bemused audience. In the current process, modellers and fishery biologists undertake the technical aspects of the assessment. The Group as a whole, however, is involved in establishing hypotheses, in agreeing to input data and parameters, and, most importantly, in examining the management implications of the assessment and identifying research needs. (As discussed above, assessment groups in the AFMA process do not make management recommendations, except in the case where there are pre-agreed decision rules.) There has therefore been considerable industry input and involvement in the assessments before the advice enters the decision-making process. With strong ownership of the assessment, agreeing and implementing management actions is generally less contentious.

Although the advantages of the process are extremely difficult to measure, one indicator may be that even though assessments for some species (e.g. eastern gemfish and orange roughy) have been extremely contentious, none of the TACs set by AFMA have been the subject of court challenges, whereas there have been numerous legal challenges to other issues in the fishery (Grieve and Richardson 2001).

In describing the advantages of the process we have perhaps painted a too optimistic picture. There are, of course, disadvantages, real and perceived. Stakeholders – industry, science and NGO – have occasionally made use of other avenues and forums to pursue alternative outcomes if they do not feel the assessment group's outcomes accord with their own views. This does not necessarily demonstrate a disadvantage of the process, because it almost certainly occurs in all jurisdictions. Rather it reflects the highly politicized nature of fisheries assessment and management. Nevertheless, this ability to 'step outside the system' does weaken the process and can lead to acrimony within the assessment groups.

One of the major problems with the current process is that it very resource hungry, in terms of people, time, and money. For example, each species-assessment group meets at least twice a year, SEFAG and the SEF Research Sub-committee meet twice each year, and there are also several workshops each year. The cost of running the SEF assessment process (meetings and reports only) is ~\$A360 000 per year and the bulk of this is used to cover travel to meetings. The actual cost of SEFAG is more than this, however, because the time of participants is generally not covered, and the opportunity cost of the time involved for an active fisher to attend meetings can be high.

Consequently, not all potential participants are willing to commit themselves to the process. Although one of the aims of the process is to ensure stakeholder participation, industry representatives are increasingly requesting fewer rather than more meetings. The AFMA budget for assessment work for national fisheries has not increased for almost a decade although the demands for assessment work have increased exponentially across national fisheries. AFMA is closely examining the budgets of each assessment group, encouraging efficiencies, and reducing the number of management-related research projects funded. This is, however, clearly not a long-term solution.

One of the effects of AFMA's outsourcing of assessments is that meetings have to be scheduled and funded well in advance, and, given the overlap in membership between groups, scheduling meetings becomes logistically problematic. It is generally not possible to hold meetings 'at will', as in other jurisdictions such as South Africa, in part because of the wide geographical spread of key participants.

Integrated Analysis (Fournier and Archibald 1985; Deriso *et al.* 1985; Methot 1989, 1990) has become the preferred approach to stock assessment in the SEF (e.g. Smith and Punt 1998; Punt *et al.* 2001*b*). Before this, other catch-at-age analyses (e.g. cohort analysis and virtual population analysis) and stock reduction analyses were used. Reasons why integrated analysis is preferred include the following: it can make use of a wide variety of data sources, it is sufficiently flexible to represent many hypotheses about the population dynamics and the relationship between the data collected and the model predictions, and it does not require continuous times-series of, for example, catch-at-age data. Simulation testing also reveals that it is the most robust assessment method for a variety of SEF species (Punt, A. D. M. Smith and G Cui, unpublished). Unfortunately, in Australia and probably elsewhere, the number of experienced scientists with the technical skills needed to applied modern methods of quantitative stock assessment is limited (Lyle 1998). This is not a problem with the current assessment process, but it is an issue that has to be dealt with in the short-to-medium term.

Unlike several other jurisdictions, AFMA does not have a fisheries-wide stock-assessment plenary or formal assessment review process. Although reviews of assessments are occasionally conducted by scientists (both Australian and overseas) who were not involved in the assessments, this is not routine practice and generally occurs only if the fishery is perceived be in 'crisis'. The lack of a stock-assessment plenary and regular assessment reviews means that there is little 'cross-fertilization' among assessment groups and no consistency of approach among fisheries. This problem is compounded by the relatively limited number of experienced fisheries modellers in Australia, as is the case in many countries.

The current process in the SEF has a relatively narrow focus, dealing primarily with assessment of single species as an input to TAC setting. SEFAG is aware of this and has attempted to deal with it by starting to identify fishery-wide management objectives and indicators, and by holding workshops to address specific issues such as effects on ecosystems. The need to deal with such wider issues is becoming more pressing with the advent of environmental legislation requiring evaluation of fisheries against wider ecological criteria than just effects on target species. Nevertheless, an important on-going focus of the assessment groups is likely to remain on single species. It is hoped that as more quantitative assessments are conducted and these assessments 'stabilize', the stock assessment process may become more 'routine' for all but the most contentious species. This should make resources available for closer examination of fishery-wide issues.

Some scientists are uncomfortable with the current process. The requirement to provide annual advice means that results from 'work-in-progress' are presented prior to formal peer review and publication, and certainly faster than some would like. A consequence of this is that assessment results may change from year to year over the duration of a particular study as improvements in knowledge and methods occur, even in the absence of 'new' data. This can be confusing and alarming to other stakeholders, and tends to result in discrediting of the scientific process. Scientists feel 'vulnerable' and other stakeholders have had to learn that, if they want the most recent results in the assessment, they have to accept that the assessment may change from one year to the next as knowledge accumulates within a particular project. When this results in recriminations or mistrust, scientists can become unwilling for their work to be included until it is formally reviewed. In addition, some scientists feel that the outcomes of the process are less conservative than they would like (Tilzey and Rowling 2001).

Some participants distrust the process; for example, some participants believe that some industry members are involved in the assessment process only as a means to advance their interests, e.g. by raising uncertainties about assessments. These interests are not always to promote higher TACs but can also involve the promotion of cross-sectoral issues (often trawl *v.* non-trawl in the SEF). However, it would be naïve to believe that industry representatives are the only ones who may participate in an assessment process to promote their interests. For example, it is well known that the probability of having a research project funded is improved substantially by lobbying and making sure that Research Plans and the like include pet projects. Participation in an assessment group is an excellent way to ensure this. This is a real issue and has to be managed closely within each assessment group. However, stakeholder influences at assessment group meetings are relatively transparent and can hence be subject to discussion (and comment in reports). In any case, this form of manipulation, to the extent it occurs, is definitely preferable to the 'last to visit the Minister' approach that has clearly been part of fisheries (and other resource) management, worldwide.

An important issue arising from the wider participation in the stock-assessment process has been how to deal with 'anecdotal' information, including individual observations by fishers (Smith *et al.* 1999; Baelde 2001). Put more simply, how do we integrate 'anecdote' with hard science? Some would say, of course, that there is no role for anecdotal information in science and quantitative assessment. SEFAG does not take such a narrow view. If industry and others are to be involved in the process they must be able to have their say and be taken seriously. Often, anecdotes are useful in helping to frame hypotheses and provide insights into the resource and how it behaves. Such anecdotal information can also lead to more serious attempts to collect relevant data, including formalizing collection of certain types of data by fishers themselves. SEFAG is not required to present a single, agreed, assessment of a species and it is common to present several scenarios, some of these being based on interpretation of the anecdotal views of industry.

Despite some clear improvements and successes over the past ten years, the SEF assessment process faces some important challenges. Chief among these is the need to deal with the demands of assessing the wider ecological effects of fishing to achieve environmental 'certification'. Nevertheless, further improvements to the stock-assessment and management process are also required. These will include the development of fishery-independent surveys to reduce reliance on commercial catch-and-effort data in constructing indices of abundance. Given the expense of such surveys and the limited value of the fishery, this approach will clearly require significant involvement by and contributions from commercial fishers. The second major focus in the short term is likely to be further development of the Management Strategy Evaluation approach (Smith 1994; Punt *et al.* 2001*a*), to address issues such as robust assessment techniques, development of robust indicators where data are limited, evaluation of 'optimal' monitoring strategies, and evaluation and implementation of decision rules and harvest strategies.

Acknowledgments

Doug Butterworth, Vivian Haist, Ken Patterson, Jake Rice, Paul Starr, and Max Stocker are thanked for extensive information regarding the assessment processes in South Africa, Canada, New Zealand and Europe. We also thank the members of SEFAG and the other SEF assessment groups for valuable discussions over the years. In particular, we acknowledge Dr Jeremy Prince for his contribution to the SEF assessment process.

References

Annala, J. H., Sullivan, K. J., and O'Brien, C. J. (Comps) (1999). Report from the Fishery Assessment Plenary, April 1999: stock assessments and yield estimates. (NIWA Greta Point library: Wellington.)

Baelde, P. (2001). Fishers' description of changes in fishing gear and fishing practices in the Australian South Eastern Trawl Fishery. *Marine and Freshwater Research* **52**, 411–17.

Blackburn, M. (1978). Changes in size composition, indicative of stock conditions in the New South Wales trawl fishery, from 1945/46 to 1966/67. CSIRO Division of Fisheries and Oceanography, Report No. 97. (CSIRO Division of Fisheries and Oceanography: Cronulla.)

Butterworth, D. S., Cochrane, K. L., and De Oliveira, J. A. A. (1997). Management procedures: a better way to manage fisheries? The South African experience. In 'Global Trends: Fisheries Management'. (Eds E. L. Pikitch, D. D. Huppert and M. P. Sissenwine.) pp. 83–90. (American Fisheries Society: Bethesda, MD.)

Chesson, J. (Ed.) (1996). The South East Fishery 1995. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Chesson, J. (Ed.) (1997). The South East Fishery 1996. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Colefax, A. N. (1938). A preliminary investigation of the natural history of the tiger flathead (*Neoplatycephalus macrodon*) on the south-eastern Australian coast. II. *Proceedings of the Linnaean Society of NSW* **63**, 155–64.

Corton, A. (1996). The widening gap between fisheries biology and fisheries management in the European Union. *Fisheries Research* **27**, 1–15.

Deriso, R. B., Quinn, T. J. II, and Neal, P. R. (1985). Catch–age analysis with auxiliary information. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 815–24.

Fairbridge, W. S. (1948). The effect of the war on the eastern Australian trawl fishery. *Journal of the Council of Scientific and Industrial Research* **21**, 75–98.

Fairbridge, W. S. (1951). The New South Wales tiger flathead, *Neoplatycephalus macrodon* (Ogilby). I. Biology and age determination. *Australian Journal of Marine and Freshwater Research* **2**, 117–78.

Fairbridge, W. S. (1952). The New South Wales tiger flathead, *Neoplatycephalus macrodon* (Ogilby). II. The age composition of the commercial catch, overfishing of the stocks, and suggested conservation. *Australian Journal of Marine and Freshwater Research* **3**, 1–31.

Fournier, D., and Archibald, C. P. (1982). A general theory for analyzing catch at age data. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1195–207.

Graham, K. J., Winstanley, R. H., and Wilson, M. A. (1982). Fishery Situation Report No. 9: Trawl and Danish seine fishery. (CSIRO Marine Laboratories: Cronulla.)

Grieve, C., and Richardson, G. (2001). Recent history of Australia's South East Fishery; a manager's perspective. *Marine and Freshwater Research* **52**, 377–86.

Han, V. C. F. (1964). Studies on the biology of the jackass fish, *Nemadactylus macropterus* Bloch and Schneider (1801) MSc Thesis, University of Sydney.

Houston, T. W. (1955) The New South Wales Trawl fishery: review of past course and examination of present condition. *Australian Journal of Marine and Freshwater Research* **6**, 165–208.

Knuckey, I. A., Grieve, C., and Smith, D. C. (1999). Evolution of the integrated scientific monitoring programme in Australia's South East Fishery. In 'Proceedings of the International Conference on Integrated Fisheries Monitoring, Sydney, Australia. 1–5 February 1999'. (Ed. C. P. Nolan.) pp. 231–48. (FAO: Rome.)

Lyle, J. (Comp.) (1998). Providing stock assessments for Australia fisheries. (Australian Society for Fish Biology, Tasmanian Aquaculture and Fisheries Institute: Hobart.)

Methot, R. (1989). Synthetic estimates of historical abundance and mortality for northern anchovy. *American Fisheries Society Symposium* **6**, 66–82.

Methot, R. (1990). Synthesis model: an adaptable framework for analysis of diverse stock assessment data. *Bulletin of the International North Pacific Fisheries Commission* **50**, 259–77.

Morison, A. K., Robertson, S. G., and Smith, D. C. (1998). An integrated system for production fish ageing: image analysis and quality assurance. *North American Journal of Fisheries Management* **18**, 587–98.

Prince, J., Baelde, P., and Wright, G. (1999). Synthesis of industry information on fishing patterns, technological change and the influence of oceanographic effects on SEF fish stocks. Report of FRDC 97/114. (FRDC: Canberra.)

Punt, A. E. (1999). Evaluating the costs and benefits of alternative monitoring programmes for fisheries management. In 'Proceedings of the International Conference on Integrated Fisheries Monitoring, Sydney, Australia. 1–5 February 1999'. (Ed. C. P. Nolan.) pp. 209–22. (FAO: Rome.)

Punt, A. E., and Smith, A. D. M. (1999). Harvest strategy evaluation for the eastern stock of gemfish (*Rexea solandri*). *ICES Journal of Marine of Science* **56**, 860–75.

Punt, A. E., Smith, A. D. M., and Cui, G. (2001*a*). Review of progress in the introduction of management strategy evaluation (MSE) approaches in Australia's South East Fishery. *Marine and Freshwater Research* **52**, 719–26.

Punt, A. E., Smith D. C., Thomson, R. B., Haddon, M., He, X., and Lyle, J. M. (2001*b*). Stock assessment of the blue grenadier *Macruronus novaezelandiae* resource off south-eastern Australia. *Marine and Freshwater Research* **52**, 701–17.

Ross, D. M., and Smith, D. C. (1997). The Australian orange roughy fishery: a process for better resource management. In 'Developing and Sustaining World Fisheries Resources: the State of Science and Management, Proceedings of the 2nd World Fisheries Conference'. (Eds D. A. Hancock, D. C. Smith, A. Grant and J. Beumer.) pp. 256–60. (CSIRO Publishing: Melbourne.)

Smith, A. D. M. (1994). Management strategy evaluation – the light on the hill. In 'Population Dynamics for Fisheries Management. Australian Society for Fish Biology Workshop Proceedings, Perth, 24–25 August 1993'. (Ed. D. A. Hancock.) pp. 249–53. (Australian Society for Fish Biology: Perth.)

Smith, A. D. M., and Punt, A. E. (1998). Stock assessment of gemfish (*Rexea solandri*) in eastern Australia using maximum likelihood and Bayesian methods. In 'Fisheries Stock Assessment Models'. (Eds T. J. Quinn II, F. Funk, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan and C-I Zhang.) pp. 245–86. (Alaska Sea Grant College Program, AK-SG-98-01: Fairbanks.)

Smith, A. D. M., and Wayte, S. E. (Eds) (2000). The South East Fishery 1999. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Smith, A. D. M., and Wayte, S. E. (Eds) (2001). The South East Fishery 2000. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Smith, A. D. M., Sainsbury, K. J., and Stevens, R. A. (1999). Implementing effective fisheries management systems – management strategy evaluation and the Australian partnership approach. *ICES Journal of Marine Science* **56**, 967–79.

Smith, D. C. (1991). South eastern trawl fishery: inshore resources. In 'Australian and New Zealand Southern Trawl Fisheries Conference: Issues and Opportunities, Melbourne, 6–9 May 1990'. (Eds K. Abel, M. Williams and P. Smith.) pp. 241–50. Bureau of Rural Resources Proceedings No. 10. (Bureau of Rural Resources: Canberra.)

Smith, D. C., Gilbert, D. J., Gason, A., and Knuckey, I. (1997). Design of an integrated scientific monitoring programme for the South East Fishery. (Australian Fisheries Management Authority: Canberra.)

Staples, D. J., and Tilzey, R. D. J. (Eds) (1995). The South East Fishery 1994. Fisheries Resources Assessment Series. (Bureau of Resource Sciences; Canberra.)

Staples, D. J., Smith D. C., and Lyle J. M. (Eds) (1994). The South East Fishery 1993. Fisheries Resources Assessment Series. (Bureau of Resource Sciences: Canberra.)

Tilzey, R. D. J. (Ed.) (1994) The South East Fishery: a scientific review with reference to quota management. (Australian Government Publishing Service: Canberra.)

Tilzey, R. D. J. (Ed.) (1998) The South East Fishery 1997. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Tilzey, R. D. J. (Ed.) (1999) The South East Fishery 1998. Fisheries Assessment Report compiled by the South East Fishery Stock Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Tilzey, R. D. J., and Rowling, K. R. (2001). History of Australia's South East Fishery: a scientist's perspective. *Marine and Freshwater Research* **52**, 361–75.

Manuscript received 5 December 2001; revised and accepted 20 February 2001

Mar. Freshwater Res., 2001, **52**, 683–90

Assessments of species in the Australian South East Fishery can be sensitive to the method used to convert from size- to age-composition data

André E. Punt[AC] *and David C. Smith*[B]

[A]CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia
[B]Marine and Freshwater Resources Institute, Department of Natural Resources and Environment, PO Box 114, Queenscliff, Vic. 3225, Australia
[C]Contact address: School of Aquatic and Fisheries Sciences, Box 355020, University of Washington, Seattle, WA 98195-5020, USA

Abstract. Information about the age-structure of the catch is one of the primary inputs to many of the methods of stock assessment currently applied to SEF species. Two methods for calculating the catch-, mean length-, and mean mass-at-age matrices from the data collected from the fishery are outlined. These methods are illustrated by applying them to data for blue grenadier, *Macruronus novaezelandiae*, and eastern school whiting, *Sillago flindersi*. The assessment and risk analysis results for blue grenadier are highly sensitive to the choice of method, whereas those for eastern school whiting are not. It is recommended that a method that allows for inter-annual variation in mean length- and hence mass-at-age should be the standard for SEF stock assessments but that sensitivity to alternative methods needs to be examined routinely.

Introduction

Assessments of most North Atlantic and North Sea fish stocks have been based on Virtual Population Analysis methods since the 1970s. However, until relatively recently, it is has not been possible to conduct assessments of South East Fishery (SEF) species by stock assessment methods that use the age-composition of the historical catches. This was due primarily to a lack of a time series of age-composition data. During the 1980s, sporadic collection of such data did, in fact, occur but data are available for only some parts of the SEF for one or two years for some species. With the introduction of the Scientific Monitoring Programme (SMP) and the Integrated Scientific Monitoring Programme (SMP) (Knuckey *et al.* 1999), and the establishment of the Central Ageing Facility (CAF) (Morison *et al.* 1998), data collection in the SEF has become more regular. For example, the primary objective of the CAF is the provision of age-composition data for key Australian fisheries, including the SEF. Age–length keys are now collected annually for most species together with information on the size distribution of the catches (both retained and discarded).

There are a variety of methods of fish stock assessment that can use age-composition data (Megrey 1989). However, *ad hoc* tuned VPA (Pope and Shepherd 1985; Butterworth *et al.* 1990), Extended Survivors Analysis (Shepherd 1999), and ADAPT-VPA (Gavaris 1988; Powers and Restrepo 1992) rely on age-composition data for all years of the assessment period. Therefore, even given the substantial improvement in the collection of size- and age-composition data for SEF species, it will still be many years before these methods of stock assessment can be applied regularly. In the short to medium term, assessments of SEF species will have to be based on Integrated Analysis (Fournier and Archibald 1982; Deriso *et al.* 1985; Methot 1989, 1990; Haist *et al.* 1993) as this approach does not require catch age-composition data for all years. Integrated Analysis may, in any case, be preferable to the other three approaches because it is more flexible as it can incorporate a wide variety of data types. Integrated Analysis has been used to assess blue grenadier, *Macruronus novaezelandiae* (Punt *et al.* 2001), eastern gemfish, *Rexea solandri* (Smith and Punt 1998), blue warehou, *Seriolella brama* (Punt 1999*a*), eastern school whiting, *Sillago flindersi* (Punt 1999*b*), and gummy shark, *Mustelus antarcticus* (Punt 1999*c*). Although the implementation of Integrated Analysis is always species-specific, it is generally the case that the likelihood function includes contributions for the catch biomass, the catch proportion-at-age, and the catch rate (assumed to be related to the exploitable biomass).

The length structure of the catch, the total mass of fish landed, and an age-length key are collected from the fishery each year to estimate the age composition of annual catches and the mean length and mass of each age-class in the catch (the catch-at-age, mean length-at-age and mean mass-at-age matrices respectively). In many instances, an average relationship between age and length is available, based on

10.1071/MF99129 1323-1650/01/040683

an analysis of several years of ageing information. A relationship between length and mass is also available. There are several methods of combining this information to calculate catch-, mean length- and mean mass-at-age matrices and, unfortunately, these can, on occasion, lead to quite different results. In this paper, two such methods that have been used for SEF species are documented and it is shown that the results of stock assessments and risk analyses can be extremely sensitive to the particular method chosen. The underlying rationale for each of the two methods is then discussed along with their advantages and disadvantages and suggestions are made related to conducting future age-based stock assessments.

Methods

The two methods for estimating catch-at-age

Prior to describing how the two methods differ, it is necessary to outline some basic notation and, in particular, to distinguish between data collected from the fishery and quantities determined from these data. The derivations below assume that the fishery consists of a single gear-type only. In reality, there is usually more than one gear-type but this complication has been ignored here for presentational simplicity. Some of the complications associated with multi-gear-type fisheries will be highlighted below. The subscripts y, l, and a refer to year, length-class and age, respectively.

Data collected from the fishery

(a) Age–length key: $A_{y,l,a}$ is the proportion of the catch during year y in length-class l that is of age a, i.e. the standard age–length key modified so that $\sum_a A_{y,l,a} = 1$.

(b) Length–frequency: $L_{y,l}$ is the proportion of the catch during year y in length-class l.

(c) Catch in mass: $\tilde{C}_y$ is the mass of fish landed during year y.

(d) Length–mass relationship: $\hat{w}_l$ is the mean mass of a fish in length-class l. This relationship is obtained by regressing the mass of individual fish in the catch on their lengths. For SEF species, the length–mass relationship is assumed to be time-invariant because the data needed to estimate it are not collected annually. $\hat{w}_l$ is therefore determined using the equation:

$$\hat{w}_l = \mathrm{e}\tilde{L}_l^{\,f}$$

where $\tilde{L}_l$ is the mid-point of length-class l, and e and f are the parameters of the length–mass relationship.

(e) Age–length relationship: $\hat{L}_a$ is the mean length of a fish of age a. This relationship is determined by fitting a standard (for example, von Bertalanffy) growth curve to many years of ageing information:

$$\hat{L}_a = \ell_\infty\left(1 - \mathrm{e}^{-\kappa(a - t_0)}\right)$$

where ℓ_∞, κ and t_0 are the parameters of the von Bertalanffy equation.

(f) Age–mass relationship: $\hat{w}_a$ is the mean mass of a fish of age a. This relationship is determined by converting the mean length-at-age from the age–length relationship to mean mass based on the length–mass relationship, i.e.:

$$\hat{w}_a = \mathrm{e}\left\{\ell_\infty\left(1 - \mathrm{e}^{-\kappa(a - t_0)}\right)\right\}^f.$$

Derived quantities

(a) Catch-at-age: $C_{y,a}$ is the catch (in number) of fish of age a during year y.

(b) Catch-at-length: $C_{y,l}$ is the catch (in number) of fish in length-class l during year y.

(c) Catch: C_y is the total catch (in number) during year y.

(d) Proportion-at-age: $p_{y,a}$ is the proportion of the catch (in number) during year y that is of age a.

(e) Mean mass of individual fish: $\bar{w}_y$ is the mean mass of individual fish in the catch during year y.

(f) Mean mass (by age): $\bar{w}_{y,a}$ is the mean mass of individual fish of age a in the catch during year y.

(g) Mean length (by age): $\bar{L}_{y,a}$ is the mean length of individual fish of age a in the catch during year y.

Basic relationships

Five relationships among the various quantities are fundamental to both methods.

(a) The proportion of the catch (in number) during year y that is of age a is calculated by multiplying the age–length key by the length–frequency to obtain the proportion of the catch by length-class and age, and then summing across lengths:

$$p_{y,a} = \sum_l A_{y,l,a} L_{y,l}\,.$$

(b) The mean mass of individual fish in the catch is obtained by averaging the mean mass of each age in the catch weighting each age by the proportion that it makes up of the catch (in number):

$$\bar{w}_y = \sum_a p_{y,a}\bar{w}_{y,a}\,.$$

(c) The catch (in number) is calculated by dividing the catch (in mass) by the mean mass of individual fish in the catch:

$$C_y = \tilde{C}_y / \bar{w}_y\,.$$

(d) The catch-at-length for year y and length-class l, $C_{y,l}$, is calculated by multiplying the total catch in number for year y by the proportion that falls into length-class l during that year:

$$C_{y,l} = C_y L_{y,l}\,.$$

(e) The catch-at-age for year y and age a, $C_{y,a}$, is calculated by multiplying the total catch in number for year y by the proportion that is age a during that year:

$$C_{y,a} = C_y p_{y,a}\,.$$

Alternative methods for estimating catch-at-age

Method 1 assumes that mean length-at-age and hence mean mass-at-age is independent of time and equal to the values predicted from the age–length and age–mass relationships, i.e.:

$$\bar{L}_{y,a} = \hat{L}_a;\ \bar{w}_{y,a} = \hat{w}_a\,. \tag{1}$$

Method 2 assumes that the mean length-at-age and mean mass-at-age may change with time and hence determines $\bar{w}_{y,a}$ and $\bar{L}_{y,a}$ directly from the data collected from the fishery during year y, i.e.:

$$\bar{L}_{y,a} = \frac{\sum_l A_{y,l,a} L_{y,l} \tilde{L}_l}{\sum_l A_{y,l,a} L_{y,l}};\ \bar{w}_{y,a} = \frac{\sum_l A_{y,l,a} L_{y,l} \hat{w}_l}{\sum_l A_{y,l,a} L_{y,l}} \text{ so that } \bar{w}_y = \sum_l A_{y,l,a} L_{y,l}\hat{w}_l\,. \tag{2}$$

The essential difference between the two methods is that Method 1 ignores the information on annual mean length- and mass-at-age that can be determined from the fishery data, whereas Method 2 ignores the age–length relationship. Note that there is no difference between the two methods in terms of how the $p_{y,a}$ data are computed.

How the two methods impact an application of Integrated Analysis

The ways in which the two methods for estimating catch-at-age affect the results of an Integrated Analysis are determined by the exact formulation of the Integrated Analysis. For the variants of Integrated Analysis considered in this paper, the effects arise primarily through the following:

(a) Selectivity. Selectivity is assumed to be a function of length. The selectivity of a given age during a given year, $S_{y,a}$, is determined from the mean length-at-age during that year ($\bar{L}_{y,a}$). If mean length-at-age is determined by Method 1, selectivity will a function of age but not of time (because $\bar{L}_{y,a}$ is assumed to be independent of year, Eqn 1). In contrast, if mean length-at-age is determined by Method 2, selectivity will be a function of both age and time.

(b) Exploitable/mature biomass. These quantities are functions of mass-at-age so will differ depending on whether Method 1 or 2 is applied. Fishing mortality is defined as the ratio of the catch to the exploitable biomass so it too will be affected by the choice of method for estimating catch-at-age.

Results and discussion

Applications to existing data sets

Table 1 lists the percentage of the catch of blue grenadier in western Bass Strait (by number) by age-class for 1997 and 1998, the mean mass of each age-class for each of the two methods, and the resulting catch-at-age. The difference in the total catch in number between the two methods for 1997 is slight (5%). However, there is a marked difference between the two methods in the total catch in number for 1998 (28%). This is a result of a 200 g difference in the mean mass of individual fish in the catch for Methods 1 and 2 (1.1 kg compared with 900 g). This difference is primarily a result of the difference between the observed mean mass (706 g) and that expected from the age–mass relationship (1.02 kg) for the highly abundant 1994 year-class (4-year-olds in 1998). Had the 4-year-olds in 1998 weighed 1.0 kg, the difference in total catch-in-number between Methods 1 and 2 would have only been 7%.

There are major differences between Methods 1 and 2 in terms of the mean mass for other age-classes. For example, the observed mean mass of a 5-year-old in 1998 (752 g) is less than that of a 4-year-old according to the age–mass relationship (1.02 kg). Furthermore (somewhat surprisingly), the mean mass of a 5-year-old in 1998 (752 g) is less than that of a 4-year-old in 1997 (1.33 kg) (i.e. fish of the 1993 year-class appear to have 'shrunk' from 1997 to 1998). This is, however, probably an artefact of ageing error whereby animals from the abundant 1994 year-class have been assigned to the much weaker 1993 year-class. It can be shown that a reduction in the estimated mean mass of 5-year-olds in 1998 from 1.3 kg to 750 g can arise if only 10–15% of the 4-year olds in 1998 are mis-aged as 5-year-olds.

Figure 1 explores differences in growth for blue grenadier among year-classes further by plotting the mean length-at-age by year-class. Quite marked differences between the observed mean length-at-age and the von Bertalanffy mean length-at-age are evident. The results for recent years (1992–95 year-classes) indicate that the weaker year-classes grow faster (the 1992 and 1993 year-classes were particularly weak, whereas the 1994 and 1995 year classes were particularly strong (Punt *et al.* 2001)). This may, however, simply be an artefact of noisy data as the 1985–87 year-classes were strong and the 1988–91 year-classes were weak but neither showed evidence of deviation from the von Bertalanffy relationship (Fig. 1). However, this may indicate that density-dependent growth only affects very strong or very weak year-classes so only assessments for species that exhibit very large fluctuations in year-class strength are likely to be very sensitive to the method used to calculate the catch-at-age data.

Figure 2 shows time-trajectories (1979–98) of (female) spawner biomass and year-class strength for blue grenadier based on Methods 1 and 2. These time-trajectories were based on the application of an Integrated Analysis estimation procedure to catch, catch rate and catch-at-age data (see Punt *et al.* 2001 for details). Although the overall trend in spawner biomass and year-class strength is qualitatively robust to the method chosen to determine mean length- and mass-at-age, there are notable quantitative differences between the two sets of results. The most noticeable difference relates to the size of the 1994 year-class. This is perhaps not surprising because the observed mean length-at-age for this strong year-class deviates quite markedly from the von Bertalanffy growth curve (Fig. 1*b*). Figure 3 shows the results of future projections based on the results in Fig. 2. Although the 'shapes' of the risk profiles are similar, there are marked quantitative differences between the results for the two methods. If not having a greater than 50% probability of dropping below 40% of B_0 is chosen as a threshold, then the constant Total Allowable Catch, *TAC*, for the next 20 years would be no larger than 11 000 t if the results from Method 1 are used. In contrast, a *TAC* of 15 000 t would be consistent with this risk criterion if the results from Method 2 are used.

Figure 4 shows time-trajectories (1991–98) of relative egg production for eastern school whiting based on Integrated Analysis. In contrast to the situation for blue grenadier, there is very little obvious difference between the results for the two methods. Furthermore, once account is taken of estimation precision, the differences can be easily ignored.

Figures 2–4 show the effect of mass-at-age changing over time. The effect is clearly case-specific, although whether it is species-specific or a function of year-class strength cannot be determined. However, even if the mean length- and mass-at-age of the population remain the same over time, changes in the gear configuration of the fishery can result in changes over time in the estimated mean length-at-age of the catch. This is illustrated in Fig. 5, which plots mean length-at-age for gummy shark and school shark *Galeorhinus galeus* caught by 6- and 7-inch-mesh gill-nets. Figure 5 shows clearly that, for young animals, the mean size of fish for a given age is lower for 6-inch gill-nets than for 7-inch gill-nets. This is because 6-inch gill-nets select for smaller fish (Kirkwood and Walker 1986). The complex effects of mesh-size on mean length-at-age in the population and catch for gummy shark are explored by Walker *et al.*

Table 1. Percentage of the catch of blue grenadier in western Bass Strait (by number) by age-class for 1997 and 1998, the mean mass of each age-class (kg) based on each of the two methods and the resulting catch-at-age

The row 'Difference' indicates the percentage difference between the mean masses-at-age computed according to the two methods. The catches-in-mass for 1997 and 1998 were 1407 and 2079 t, respectively

	Age																				Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
										1997											
Percentage, $p_{y,a}$	0.44	16.42	37.70	3.82	6.89	3.67	2.13	2.61	6.71	8.59	3.04	2.67	2.13	0.19	0.20	1.03	0.40	1.09	0.09	0.17	
Method 1																					
Mass-at-age, $\hat{w}_a$	0.167	0.400	0.697	1.019	1.340	1.641	1.912	2.149	2.353	2.526	2.670	2.789	2.887	2.967	3.032	3.085	3.128	3.163	3.191	3.213	
Catch-at-age, $C_{y,a}$	4486	167206	384037	38905	70169	37425	21689	26580	68378	87512	30970	27229	21674	1907	2059	10475	4090	11085	907	1761	1018544
Method 2																					
Mass-at-age, $\bar{w}_{y,a}$	0.371	0.480	0.614	1.332	2.000	2.033	2.576	2.595	2.523	2.363	2.578	2.657	2.626	2.997	3.050	3.020	4.060	3.247	3.965	4.370	
Catch-at-age, $C_{y,a}$	4736	176533	405460	41076	74083	39513	22899	28063	72192	92393	32697	28748	22883	2014	2174	11060	4318	11704	958	1860	1075363
Difference	122.32	20.00	–11.80	30.64	49.24	23.90	34.75	20.71	7.22	–6.46	–3.45	–4.73	–9.02	0.99	0.58	–2.13	29.80	2.66	24.26	36.00	
										1998											
Percentage, $p_{y,a}$	0.00	0.88	23.74	53.86	11.35	2.36	0.38	0.23	0.27	1.20	1.88	1.85	1.25	0.29	0.14	0.26	0.03	0.02	0.00	0.01	
Method 1																					
Mass-at-age, $\hat{w}_a$	0.167	0.400	0.697	1.019	1.340	1.641	1.912	2.149	2.353	2.526	2.670	2.789	2.887	2.967	3.032	3.085	3.128	3.163	3.191	3.213	
Catch-at-age, $C_{y,a}$	0	16358	441343	1001233	211015	43862	7013	4332	5034	22333	34989	34419	23181	5482	2562	4771	525	286	76	274	1859087
Method 2																					
Mass-at-age, $\bar{w}_{y,a}$	n.a.	0.518	0.661	0.706	0.752	1.645	2.250	2.741	2.785	2.510	2.614	2.523	3.202	2.924	2.745	2.159	2.979	3.573	3.632	3.594	
Catch-at-age, $C_{y,a}$	0	20938	564896	1281527	270089	56141	8977	5544	6444	28585	44784	44055	29670	7017	3279	6106	672	366	97	351	2379536
Difference	n.a.	29.45	–5.05	–30.69	–43.84	0.28	17.69	27.53	18.36	–0.62	–2.09	–9.55	10.90	–1.45	–9.47	–30.01	–4.77	12.97	13.84	11.86	

n.a., not applicable.

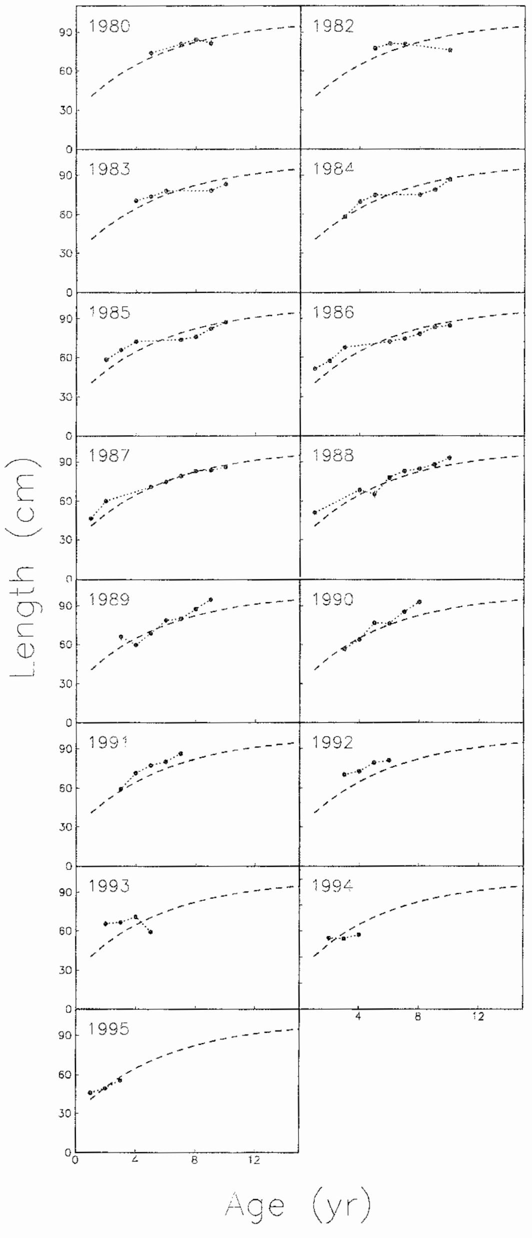


Fig. 1. Mean length at age (with one standard deviation) by year-class for blue grenadier. The dashed line denotes the results of a fit of a von Bertalanffy growth curve to all of the ageing data for blue grenadier.

(1998). If the data in Fig. 5 were used in an assessment, error would occur if the effect of selectivity on length-at-age was ignored.

The problem that the results of assessments depend on how the catch-, mean length- and mean mass-at-age matrices are constructed is clearly an issue for the SEF. However, Method 1 has been used extensively in South Africa (e.g. Punt 1994) and New Zealand (Hanchet 1997; Davies 1998) so this problem is definitely not restricted to the SEF.

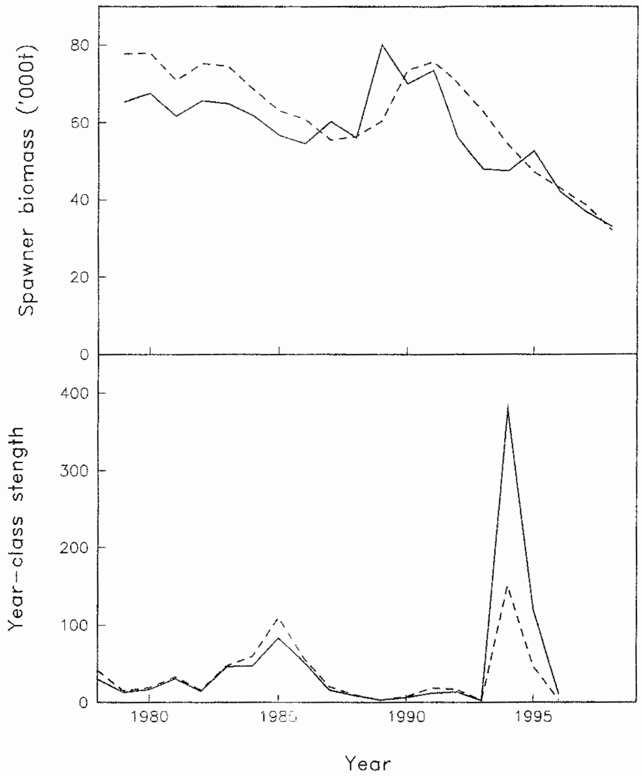


Fig. 2. Time-trajectories of (female) spawner biomass and year-class strength for blue grenadier based on Methods 1 (dashed lines) and 2 (solid lines). Source: Punt *et al.* (2001).

Selecting between the methods

The difference between Methods 1 and 2 relates to assumptions regarding errors. Method 1 assumes that any differences between mean mass-at-age from the age–length key/length–frequency and that from the age–mass relationship are a consequence of observation error, whereas Method 2 assumes that the differences are real and hence that there may be substantial 'process' error. An alternative explanation to changes over time in mass- and length-at-age for the population is that selectivity-at-length changes over time.

Mean mass-at-age can differ between the Methods by up to 30–50% (Table 1). However, the difference between Methods 1 and 2 in the estimates of the strength of the 1994 year-class for blue grenadier greatly exceeds this (Fig. 2). Assessments of SEF species are often based on the assumption that selectivity is length-dependent but time-invariant (e.g. Smith and Punt 1998; Punt *et al.* 2001). If mean length-at-age changes over time, this will imply changes over time in selectivity-at-age even though selectivity as a function of length is time-invariant. This effect is the other main cause for the major differences in the estimates of the strength of the 1994 year-class of blue grenadier between Methods 1 and 2. An assessment based

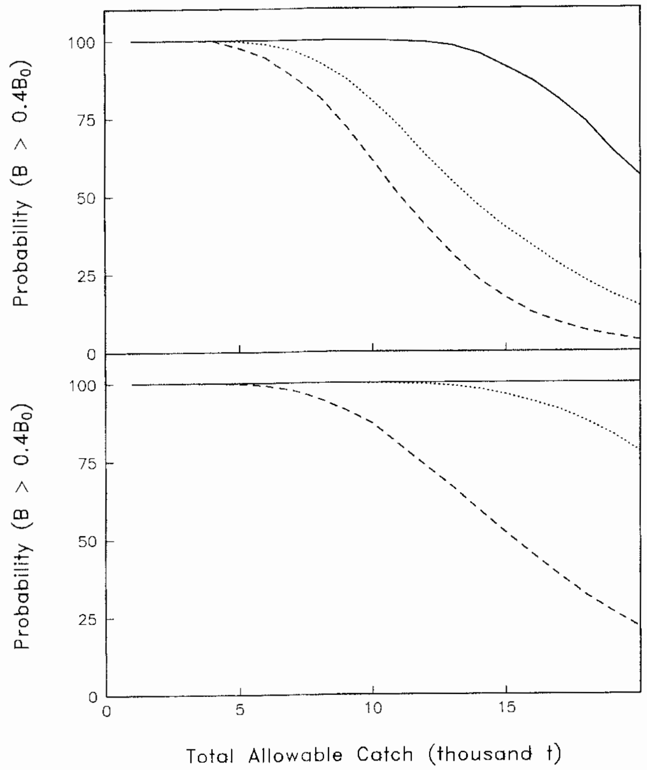


Fig. 3. Probability of the (female) spawner biomass not dropping below 40% of B_0 as a function of the level of future Total Allowable Catch. Results are shown for 5 (solid lines), 10 (dotted lines), and 20 year (dashed lines) projection periods. The results for Method 1 are shown in the upper panel and those for Method 2 in the lower panel. Source: Punt *et al.* (2001).

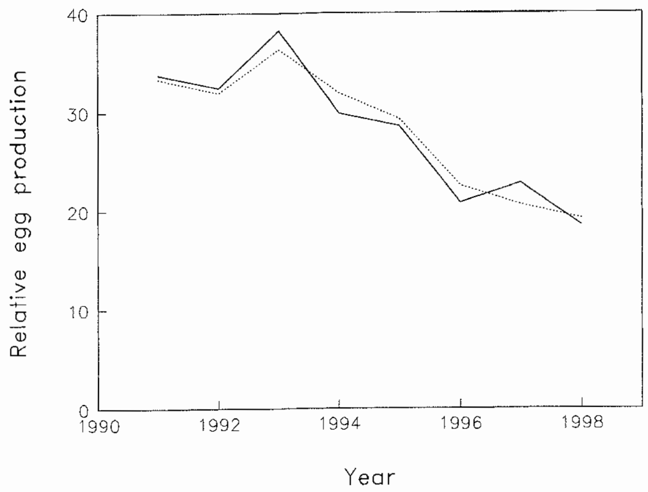


Fig. 4. Time-trajectories of relative egg production for eastern school whiting based on Methods 1 (dashed line) and 2 (solid line) (see Punt 1999*b* for details of the assessment method applied).

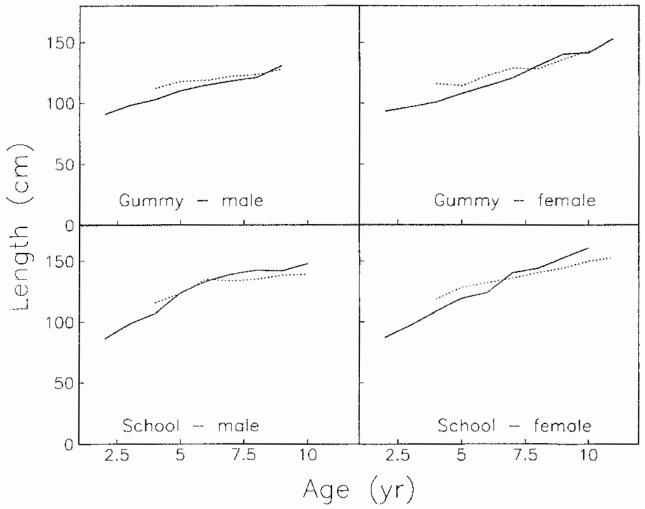


Fig. 5. Mean length-at-age for catches of gummy and school shark in Bass Strait (1990–93) by sex. Results are shown for catches by 6-inch (solid lines) and 7-inch (dotted lines) gill-nets.

on Method 1 assumes that the mean length-at-age of the 1994 year-class is equal to that expected from the age–length relationship and hence animals of this year-class should be relatively well selected (given the estimated length-specific selectivity pattern). In contrast, an assessment based on Method 2 that sets the mean length-at-age for the 1994 year-class to the observed value would assume that this year-class should be less well selected.

We recommend that Method 2 be the standard approach for stock assessments in the SEF. This is because only it is capable of allowing for time-dependence in length- and mass-at-age. This is also the approach that is generally used to construct catch-at-age matrices for North Atlantic and North Sea species. However, we also recommend that sensitivity to applying Method 1 be considered routinely. This is because Method 2 is subject to several uncertainties, as described below, and because the results (particularly for projections) may be sensitive to the choice of Method. Furthermore, we recommend that the following standard diagnostics be considered when conducting future assessments.

(a) The precision of the estimates of quantities of interest to management.

If the assumption regarding mass-at-age was incorrect, the estimated variance of quantities of interest to management would be greater. For blue grenadier, however, there is no clear difference between assessments based on the two methods in the coefficients of variation for the estimates of the virgin and current spawner biomasses, the two key model outputs.

(b) The fit to the catch (in number) information.

If the assumptions regarding mean mass-at-age are poor, the residuals from such fits are likely to exhibit systematic patterns.

(c) Whether the mean lengths- and masses-at-age behave sensibly biologically.

For example, Method 2 could result in the mean length of some year-classes dropping with age. While this does occur in reality (see Fig. 1), wild fluctuations in mean length-at-age would suggest that the sample sizes for the age-length key and/or the length frequency are too low.

Both methods, however, clearly have problems. The first method is based on the assumption that mean length- and mass-at-age (and consequently selectivity at age) are independent of time. This assumption will not be correct for a variety of reasons. These include changes in mean length-at-age with density. The second method has the disadvantage that the precision of its estimates of mean length- and mass-at-age change annually because this depends on the sample sizes for the age–length key and length–frequency distribution. Other problems with the second method relate to how to calculate biomasses from population models (e.g. spawner biomass, recruited biomass) when applying Integrated Analysis. This is because mass-at-age will not be available for any years for which both age–length keys and length–frequencies are not available (usually the early years of exploitation). For blue grenadier, this last problem has been overcome by estimating mass-at-age for the years for which data are not available by the mean over the years for which data are available.

In addition, Method 2 is conceptually inconsistent with an Integrated Analysis estimation framework. This is because the mean length- and mean mass-at-age matrices input into the assessment are assumed to be known exactly (see, for example, Appendix A of Punt *et al.* 2001). However, these matrices are based on the same basic data as the catch-at-age matrix, which are treated as being subject to sampling error. This 'problem' could be dealt with by treating the length-at-age information as data, and using the model to predict the length-at-age each year. Apart from using the data more consistently, such an approach would also eliminate the need for rules to interpolate length- and mass-at-age for those years/ages for which actual data are not available. This approach would also (in principle) allow the effects of observation error to be discriminated from those of process error.

Method 1 is much simpler to implement, particularly for projections, because it assumes that future mass- and length-at-age is the same as that for the past. In contrast, Method 2 requires making allowance for future uncertainty in length- and mass-at-age. This problem affects assessments based on both VPA and Integrated Analysis, unlike the problem related to calculating mass-at-age for any years for which age–length keys and length–frequencies are not available, which is specific to Integrated Analysis. To date, projections for assessments based on Method 2 have either assumed that length- and mass-at-age in the future is equal to the average of the observed data or uncertainty is accounted for by selecting a vector of length- and mass-at-age at random from a past year for each future year. For Integrated Analysis, however, a better, but technically more complicated, solution would be to use the results from a model that relates length- and mass-at-age to other co-variates (such as, for example, year-class strength).

This paper ignores the effect of differences over time in the length–mass relationship. Such differences could arise, for example, because of changes over time in condition factor. However, whereas Method 2 can be extended straightforwardly to allow for year-specific mean mass-at-length (by replacing $\hat{w}_l$ with $\hat{w}_{y,l}$ in Eqn 2), this extension cannot be applied in practice in the SEF because the data needed to estimate year-specific length–mass relationships are not currently collected on an annual basis.

Acknowledgments

Sandy Morison, Simon Robertson and Corey Green (CAF) provided the age–length keys for blue grenadier and school whiting, and Ian Knuckey (MAFRI) provided the length frequencies from data collected by the Integrated Scientific Monitoring Program. Terry Walker (MAFRI) is thanked for supplying the length-at-age data for gummy and school shark. Tony Smith, Robin Thomson (CSIRO Marine Research) and the members of BWAG and BGAG are thanked for their comments on earlier versions of this paper.

References

Butterworth, D. S., Hughes, G., and Strumpfer, F. (1990). VPA with *ad hoc* tuning: implementation for disaggregated fleet data, variance estimation, and application to the Namibian stock of Cape horse mackerel *Trachurus trachurus capensis*. *South African Journal of Marine Science* **9**, 327–57.

Davies, N. M. (1999). Assessment of the SNA 1 and SNA 8 stocks for the 1997–98 fishing year. New Zealand Fisheries Research Assessment Document No. 99/19. 87 pp.

Deriso, R. B., Quinn, T. J. II, and Neal, P. R. (1985). Catch–age analysis with auxiliary information. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 815–24.

Fournier, D., and Archibald, C. P. (1982). A general theory for analyzing catch at age data. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1195–207.

Gavaris, S. (1988). An adaptive framework for the estimation of population size. Canadian Atlantic Fisheries Science Advisory Committee Research Document No. 88/29. 12 pp.

Haist, V., Fournier, D. A., and Schweigert, J. F. (1993). Estimation of density-dependent natural mortality in British Columbia herring stocks through SSPA and its impact on sustainable harvesting strategies. In 'Risk Evaluation and Biological Reference Points for Fisheries Management'. (Eds S. J. Smith, J. J. Hunt and D. Rivard.) *Canadian Journal of Fisheries and Aquatic Sciences Special Publication* **120**, 269–82.

Hanchet, S. M. (1997). Southern blue whiting (*Micromesistus australis*) stock assessment for the 1996–97 and 1997–98 fishing years. New Zealand Fisheries Research Assessment Document No. 97/14. 34 pp.

Kirkwood, G. P., and Walker, T. I. (1986). Gill net mesh selectivities for gummy shark, *Mustelus antarcticus* Günther, taken in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **37**, 689–97.

Knuckey, I. A., Grieve, C., and Smith, D. C. (1999). Evolution of the integrated scientific monitoring programme in Australia's South East Fishery. In 'Proceedings of the International Conference on Integrated Fisheries Monitoring. Sydney, Australia, 1–5 February 1999'. (Ed. C. P. Nolan.) pp 281–48. (FAO: Rome.)

Megrey, B. A. (1989). Review and comparison of age-structured stock assessment models from theoretical and applied points of view. *American Fisheries Society Symposium* **6**, 8–48.

Methot, R. (1989). Synthetic estimates of historical abundance and mortality for northern anchovy. *American Fisheries Society Symposium* **6**, 66–82.

Methot, R. (1990). Synthesis model: an adaptable framework for analysis of diverse stock assessment data. *Bulletin of the International North Pacific Fisheries Commission* **50**, 259–77.

Morison, A. K., Robertson, S. G., and Smith, D. C. (1998). An integrated system for production fish ageing: image analysis and quality assurance. *North American Journal of Fisheries Management* **18**, 587–98.

Pope, J. G., and Shepherd, J. G. (1985). A comparison of the performance of various methods for tuning VPAs using effort data. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **42**, 129–51.

Powers, J. E., and Restrepo, V. R. (1992). Additional options for age-sequenced analysis. *Collective Volume of Scientific Papers ICCAT* **39**, 540–53.

Punt, A. E. (1994). Assessments of the stocks of Cape hake *Merluccius* spp. off South Africa. *South African Journal of Marine Science* **14**, 159–86.

Punt, A. E. (1999*a*). An assessment of blue warehou for 1999 based on integrated analysis. Document submitted to the 7–8 June 1999 meeting of BWAG. 37 pp.

Punt, A. E. (1999*b*). ADAPT and integrated analysis assessments of school whiting. Document submitted to the 17–18 June 1999 school whiting workshop. 18 pp.

Punt, A. E. (1999*c*). Preliminary assessment of the population of gummy shark (*Mustelus antarcticus*) in Bass Strait. SharkFAG Document SharkFAG/99/D13. 38 pp.

Punt, A. E., Smith D. C., Thomson, R. B., Haddon, M., He, X., and Lyle, J. M. (2001). Stock assessment of the blue grenadier, *Macruronus novaezelandiae* resource off south-eastern Australia. *Marine and Freshwater Research* **52**, 701–17.

Shepherd, J. G. (1999). Extended survivors analysis: an improved method for the analysis of catch-at-age data and abundance indices. *ICES Journal of Marine Science* **56**, 584–91.

Smith, A. D. M., and Punt, A. E. (1998). Stock assessment of gemfish (*Rexea solandri*) in eastern Australia using maximum likelihood and Bayesian methods. In 'Fisheries Stock Assessment Models'. (Eds T. J. Quinn II, F. Funk, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan and C-I Zhang.) pp. 245–86. (Alaska Sea Grant College Program, AK-SG-98-01.)

Walker, T. I., Taylor, B. L., Hudson, R. J., and Cottier, J. P. (1998). The phenomenon of apparent change of growth rate in gummy shark (*Mustelus antarcticus*) harvested off southern Australia. *Fisheries Research* **39**, 139–63.

Manuscript received 8 September 1999; revised and accepted 21 January 2000

Mar. Freshwater Res., 2001, **52**, 691–99

Estimating gill-net selectivity for five species caught in the South East Fishery, Australia

Gurong Cui[A], *Nicholas J. Bax*[A], *André E. Punt*[A] *and Ian A. Knuckey*[B]

[A]CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia
[B]Marine and Freshwater Resources Institute, Department of Natural Resources and Environment, PO Box 114, Queenscliff, Vic. 3225, Australia

Abstract. A formal approach to estimating selectivity patterns that allows for variability additional to Poisson sampling variability is outlined. This approach, which involves assuming that the catch of fish by a particular size of gill-net in a given size-class is distributed according to a negative binomial distribution, is applied to data for five of the species caught by experimental gill-nets in Australia's South East Fishery. The data for two of these species (blue warehou and dogfish) are not compatible with the conventional assumption that the size of fish corresponding to maximum selectivity is linearly proportional to mesh size. Selectivity and population size-structure are found to depend on depth and habitat type for some of the species. It is necessary therefore to target future experiments to depth zones/habitat types in which the bulk of the catch is taken to estimate selectivity patterns for use in stock assessments.

Introduction

Selectivity is the probability per unit fishing mortality of a fish of a given species being captured given that it encounters the fishing gear. In general, selectivity is defined as a function of the length of an individual. However, more appropriate variables include gape (for hooks), or girth (for trawl or gill-net caught fish). Information about the selectivity of different fishing gears can be used to address a variety of questions. These include selection of a gear-type that achieves the most desirable mix of species in a multi-species fishery (Murawski 1984; Sainsbury 1984; Pikitch 1987; Marchal and Horwood 1996), and identification of a gear-type that reduces by-catch and discards (Murawski 1996; Perez-Comas *et al.* 1998). Selectivity patterns can also be used directly in stock assessments. For example, Walker (1992) and Punt and Walker (1998) reduce the number of parameters in assessments of gummy shark, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*, by setting the parameters of the length-specific selectivity function to values determined from independent experiments (Kirkwood and Walker 1986).

This study extends the framework within which selectivity is conventionally estimated in the South East Fishery to formally allow for variability over and above sampling error. Such additional variability could arise if availability varies among shots, for example, for species that school or whose distributions vary diurnally. The extended framework is applied to estimate selectivity patterns for five of the species caught by experimental gill-nets in the South East Fishery (four quota species and a non-quota species; Table 1). Except for gummy shark and blue warehou, the catches by gill-net of these five species in the South East Fishery (henceforth SEF) are comparatively low. However, the takes of these target and non-target species need to be included in assessments and quantification of selectivity will substantially ease this process.

Materials and methods

Field studies

The data were collected between Point Hicks and Disaster Bay on Australia's south-east continental shelf in April 1996 (depths less than ~100 m) and January 1997 (depths greater than ~100 m) (Williams and Bax 2001). One gill-net was set at sunrise and retrieved one to two hours before sunset and another gill-net was set just after dark and retrieved prior to sunrise. Sampling locations were chosen to represent different depths and microhabitats, as determined from acoustic and video sampling (Williams and Bax 2001).

Each gill-net consisted of two fleets of six panels (one panel for each of the six mesh sizes considered in the study: 50, 75, 100, 125, 150 and 175 mm; 2 to 7 inches). The order of the panels was random but the same between sets. The panels had a hanging ratio of 0.5, and a hanging coefficient of 0.87. The monofilament line sizes were 0.62, 0.62, 0.81, 0.9, 0.9 and 1.05 for the six mesh sizes, respectively. Each panel measured 90 × 2.8 m and was separated by a 40 m gap, giving the net a total length of ~1.5 km. The ground line was heavily weighted (38 kg per panel) and the float line buoyant (11.4 kg per panel) because of the high current speeds expected in some areas. For the same reason, 20 kg grapples were used to anchor the centre and each end of the net fleet

The numbers and weights of all fish in the catch were recorded. Taxonomic identifications were based primarily on Last and Stevens (1994) and Gomon *et al.* (1994) but also relied on a set of illustrated

10.1071/MF99162 1323-1650/01/040691

field identification sheets. Lengths were measured for all species with greater than five individuals per set. Fish lengths were measured from the tip of the snout to the tip of the medial caudal-fin ray, with the caudal-fin in its natural position, and recorded as Fork Length (FL). Shark and ray species were measured from the tip of the snout to the upper caudal-fin lobe, with the caudal-fin in an extended position, and also recorded as Total Length.

The spatial distribution of shots during the experiment can be categorized according to two variables: habitat and depth. Three distinct habitats were identified: rough/reef, hard/close to reef and soft/away from reef, and the data were stratified into four depth strata: A (<40 m), B (40–69 m), C (70–99 m), and D (100–139 m). Analysis of community composition data (Williams and Bax 2001) indicates that it is possible to categorize data from hard habitats as either soft or rough depending on area and this has been done in this study. Table 1 shows a breakdown of the 36 shots conducted during the experiment according to habitat type and depth zone.

Modelling studies

A variety of methods are available to estimate selectivity. These can be direct or indirect (Regier and Robson 1966). Direct methods involve modelling the results obtained by fishing a population with a known size-structure (Regier and Robson 1966). The known population can be either a tagged population or the population susceptible to a non-selective fishing gear. Indirect methods, on the other hand, attempt to estimate the selectivity function without knowledge of the underlying size-structure of the population. As is the case in most studies (e.g. Kirkwood and Walker 1986; Punt *et al.* 1996; Hovgård *et al.* 1999), this study is based on an indirect method because the size-structure of the populations cannot be determined directly.

Following Hamley (1975), Reiger and Robson (1966) and Kirkwood and Walker (1986), the expected catch in number of fish in size (length) class j by mesh-size i during set s in habitat type h and depth zone d, $E(N_{h,d,s,i,j})$, is given by:

$$E(N_{h,d,s,i,j}) = S_{h,d,s,i,j} q_{h,d,s,i} E_{h,d,s,i} \mu_{h,d,s,j} \qquad (1)$$

where $S_{h,d,s,i,j}$ is the relative selectivity of gear-type i during set s in habitat type h and depth zone d on fish in size-class j, $E_{h,d,s,i}$ is the fishing effort for gear-type i during set s in habitat type h and depth zone d, $\mu_{h,d,s,j}$ is the expected number of fish in size-class j available to any of the gear-types during set s in habitat type h and depth zone d, and $q_{h,d,s,i}$ is a constant of proportionality (the 'catchability') for mesh-size i during set s in habitat type h and depth zone d. Equation (1) defines the product $S_{h,d,s,i,j} q_{h,d,s,i}$, but not its component terms. This ambiguity is removed by specifying that the maximum (over size-classes j) $S_{h,d,s,i,j}$ for each gill-net i is 1, hence the term 'relative' selectivity. Table 1 lists the widths of the size-classes considered for the analyses of this paper. The choices in Table 1 are based on avoiding having size-classes with insufficient data.

The dependence of the catch on habitat type and depth zone is explicitly recognized in the way that Eqn (1) has been constructed. This is because it is known that some of the species in Table 1 have habitat/depth preferences. For example, larger individuals of blue warehou tend to be found on rougher ground (Furlani *et al.*, in press). This raises the question of the extent to which data can/should be pooled across habitat/depth strata. For example, it would seem to be invalid to pool data across depth zones/habitat types if the size-composition of the population differs among these strata.

The general model is simplified by:

(a) assuming that catchability for a given habitat type and depth zone is independent of set and hence pooling data across sets (the dependence of catch, selectivity, catchability, effort and population size-structure on set is therefore suppressed in the remainder of this paper);

(b) assuming that fishing power is independent of mesh-size, i.e. $q_{h,d,s,i} = q_{h,d}$;

(c) assuming that fishing effort is independent of mesh-size, i.e. $E_{h,d,s,i} = E$ (this assumption is valid for the current study because all of the mesh-sizes were used during each shot); and

(d) representing selectivity for a given habitat type and depth zone by a simple function of the mesh-size, m_i, and the mid-point of size-class j, L_j.

The selectivity function

The selectivity function, S_{ij} (suppressing, for the moment, the possible dependence on habitat type and depth zone for ease of presentation), can be modelled by a variety of functional forms (see, for example, the review by Millar and Fryer 1999). However, for the purposes of this study, we follow Kirkwood and Walker (1986), Henderson and Wong (1991) and Pierce *et al.* (1994) and base the analysis on the assumption that S_{ij} can be represented by a gamma function, i.e.:

$$S_{i,j} = \left(\frac{L_j}{a_i b_i}\right)^{a_i} e^{a_i - L_j/b_i} \qquad (2)$$

where a_i, b_i are parameters that determine the selectivity pattern for mesh-size i.

It is assumed further (see simplification d above; Kirkwood and Walker 1986) that the size at maximum selectivity for mesh size i is linearly proportional to the mesh size, m_i, and that the variance of the selectivity function is independent of mesh-size. This permits the number of parameters needed to model selectivity to be reduced from two for each mesh-size to two in total (θ1 and θ2):

$$a_i b_i = \theta_1 m_i \qquad b_i = -0.5[\theta_1 m_i - \sqrt{\theta_1^2 m_i^2 + 4\theta_2}]\,. \qquad (3)$$

Parameter estimation

It is assumed that the catches in number (by habitat type, depth zone, mesh-size and size-class) are independent random variables drawn from a pre-specified probability distribution. This assumption leads to the following likelihood function:

$$L(N|\underline{\theta}) = \prod_{h,d,i,j} P(N_{h,d,i,j} = n_{h,d,i,j}|\underline{\phi}) \qquad (4)$$

where $n_{h,d,i,j}$ is the observed catch of animals in size-class j by mesh-size i in habitat type h and depth zone d, and $\underline{\phi}$ is the vector of model parameters. The AD Model Builder package[1] was used to find the values for the parameters that maximize the likelihood function.

Choosing a structural model

The full model (Eqn 1) assumes that selectivity, catchability and population size-structure differ among habitat types and depth zones. This model can be simplified by assuming that some of the variables are independent of habitat type or depth zone (Table 2). For some of the model formulations in Table 2, some of the catchability parameters can be subsumed in the parameters that determine population size-structure (the μs). The likelihood ratio test (Mood *et al.* 1974) is used to test whether simpler model formulations are able to provide satisfactory fits to the data compared with more complex model formulations.

Choosing a probability model

The Poisson distribution is a natural first choice for modelling count data. It is able to approximate skewed and normal-shaped distributions

---

[1] © Otter software: http://otter-rsch.com

Table 1. Catches during the experiment by depth zone and habitat type and the widths assumed for the size-classes when fitting the model used to estimate selectivity

The column 'number of size-classes' lists the number of size-classes when the data are pooled across depth zones and habitat types. The data for the habitat type–depth zone combinations indicated by asterisks are not used in the analyses owing to small sample size (<20 individuals)

Species name	Catch by depth zone and habitat zone								Total catches used	Size-class width (mm)	Number of size-classes
	Rough				Smooth						
	A	B	C	D	A	B	C	D			
Shots conducted:	3	3	0	13	0	4	4	9			
Quota species											
Mustelus antarcticus (Gummy shark)	5*	20	–	5*	–	39	190	4*	249	100	12
Seriolella brama (Blue warehou)	0*	40	–	222	–	16*	172	50	484	30	9
Neoplatycephalus richardsoni (Tiger flathead)	0*	0*	–	42	–	60	9*	132	234	50	9
Nemadactylus macropterus (Jackass morwong)	0*	0*	–	428	–	1*	75	69	572	30	8
Non-quota species											
Squalus megalops (Spiny dogfish)	0*	77	–	977	–	128	310	1223	2715	20	21

Table 2. Full selectivity model (model Ia) and submodels

Entries in the columns 'population structure' and 'selectivity' reflect the factors (apart from fish size and mesh-size as appropriate) on which the variable concerned is assumed to depend. *indicates that interaction terms are included. Catchability always depends on habitat type and depth zone to capture the effects of differences in, *inter alia*, effort among these strata

Model number	Population structure	Selectivity	Variant of Eqn 1
Ia	Habitat * depth	Habitat * depth	$S_{h,d,i,j}\mu_{h,d,j}$
Ib	Habitat * depth	Depth	$S_{d,i,j}\mu_{h,d,j}$
Ic	Habitat * depth	Habitat	$S_{h,i,j}\mu_{h,d,j}$
Id	Habitat * depth	–	$S_{i,j}\mu_{h,d,j}$
IIa	–	Habitat * depth	$S_{h,d,i,j}q_{h,d}\mu_j$
IIb	–	Depth	$S_{d,i,j}q_{h,d}\mu_j$
IIc	–	Habitat	$S_{h,i,j}q_{h,d}\mu_j$
IId	–	–	$S_{i,j}q_{h,d}\mu_j$
IIIa	Depth zone	Habitat * depth	$\mathrm{S}_{\mathrm{h,d,i,j}}\mathrm{q}_{\mathrm{h,d}}\mu_{h,j}$
IIIb	Depth zone	Depth	$S_{d,i,j}q_{h,d}\mu_{h,j}$
IIIc	Depth zone	Habitat	$S_{h,i,j}q_{h,d}\mu_{h,j}$
IIId	Depth zone	–	$S_{i,j}q_{h,d}\mu_{h,j}$

and has been used in several previous studies of the selectivity of trawls, gill-nets and hooks (e.g. Kirkwood and Walker 1986; Millar and Walsh 1992; Punt *et al.* 1996; Millar and Fryer 1999). However, the assumption underlying the choice of the Poisson distribution, that the variation in catches about the model predictions is due solely to sampling error, is unlikely to be valid in many cases. Some account can be taken of this 'additional' variability by assuming that the mean of the Poisson distribution varies according to some (pre-specified) distribution. For the purposes of this study, it is assumed that the mean of the Poisson distribution varies according to a gamma distribution. It can be shown (Johnson and Kotz 1969; McConnell and Horn 1972) that these assumptions lead to the following (negative binomial) distribution (shown here for the case in which population size-structure and selectivity are assumed to be independent of habitat type and depth zone; model IId):

$$P(N_{h,d,i,j} = n_{h,d,i,j} | \theta_1, \theta_2, \alpha, \mu_j, q_{h,d}) = \binom{\alpha + n_{h,d,i,j} - 1}{\alpha - 1} \left(\frac{q_{h,d}\,\mu_j S_{i,j}}{\alpha + q_{h,d}\,\mu_j S_{i,j}} \right)^{n_{h,d,i,j}} \left(\frac{\alpha}{\alpha + q_{h,d}\,\mu_j S_{i,j}} \right)^{\alpha} . \quad (5)$$

The variance of the negative binomial distribution, $Var\,(N_{h,d,i,j})$, is given by

$$Var\,(N_{h,d,i,j}) = q_{h,d}\,\mu_j S_{i,j} \left(1 + \frac{q_{h,d}\,\mu_j S_{i,j}}{\alpha} \right) . \quad (6)$$

The parameter α determines the extent of heterogeneity in the mean of the Poisson distribution. $Var\,(N_{h,d,i,j})$ converges to $q_{h,d}\,\mu_j S_{i,j}$, the mean of the Poisson distribution, as $\alpha \rightarrow \infty$ Therefore, as expected, the assumption that the observations are distributed according to the Poisson distribution is a special case of the general model outlined here. The choice for this study that the mean of the Poisson distribution varies according to the gamma distribution is primarily for numerical convenience and future work should consider the merits of alternatives. The negative binomial distribution has been used to model distributions of catch counts in several studies (e.g. Welch and Ishida 1993; Augustin *et al.* 1998).

For the case represented in Eqn (5), there are three parameters to represent selectivity (θ_1, θ_2, α), Q parameters to represent catchability (where Q is one less than the number of combinations of habitat type and depth zone), and one μ parameter for each of the J size-classes for a total of $3+J+Q$ parameters.

Goodness-of-fit testing

The standard χ^2 test can be used to examine the goodness-of-fit of alternative models. However, it is necessary to first transform the negative binomial distribution into a form that is approximately normal (Cui *et al.* 1999):

$$\chi^2_{n-J-Q-S} = 4 \sum_{h,d,i,j} [Y_{h,d,i,j} - E(Y_{h,d,i,j})]^2 \quad (7)$$

where $$Y_{h,d,i,j} = \sqrt{\alpha_{h,d} - \frac{1}{2}}.\sinh^{-1}\sqrt{\frac{n_{h,d,i,j} + \frac{3}{8}}{\alpha_{h,d} - \frac{3}{4}}}, \text{ and}$$

$$E(Y_{h,d,i,j}) = \sqrt{\alpha_{h,d} - \frac{1}{2}}.\sinh^{-1}\sqrt{\frac{E(N_{h,d,i,j}) + \frac{3}{8}}{\alpha_{h,d} - \frac{3}{4}}}$$

where S is the number of selectivity parameters estimated.

Under the assumption that the $N_{h,d,i,j}$ are independent random samples from the negative binomial distribution defined by Eqn (5), the statistic $\chi^2_{n-J-Q-S}$ should be a random sample from a χ^2 distribution with n-J-Q-S degrees of freedom.

Results and discussion

Choice of appropriate models

Table 3 compares fits of various submodels of the full model (Ia; Table 2) with that of the full model by means of likelihood ratio tests. Results are shown for the negative binomial and Poisson error models. The submodels considered in Table 3 examine different assumptions regarding whether selectivity depends on habitat type and depth zone. All of the models in Table 3 assume that population size-structure differs among habitat types and depth zones. The model in which selectivity is independent of both habitat type and depth zone (Model Id) is not significantly poorer at the 5% level than the full model for two species [gummy shark (both error models) and jackass morwong (Poisson error model)] only. The submodel that assumes that selectivity is independent of habitat type (Model Ic) provides fits that are poorer than that of the full model at the 1% level for three of the five species.

The likelihood ratio tests indicate that some of the submodels do not fit the data any worse than does the full model for some of the species. However, this may be an artefact because the catches are not distributed equally across depth/habitat strata. For example, 76% of the data for gummy shark were collected from the smooth-D stratum (Table 1).

The assumptions that the errors about the model fits are Poisson or negative binomially distributed are examined using the χ^2 statistic (Eqn 7) and likelihood ratio tests in Table 4. Results are shown in Table 4 for analyses based on models that assume that population size-structure differs among habitat and depth strata (Models Ia–Id) and that assume that the population size-structure is (in relative terms) the same in all habitat and depth strata (Models IIa–IId). For the negative binomial error model, three species (gummy shark, flathead and jackass morwong) satisfy the goodness-of-fit test at the 1% level for Model Ia, whereas all but dogfish satisfy it at the 1% level for Model IIa. In contrast, only the fit for gummy shark satisfies the goodness-of-fit test at the 1% level for Model IIa for the Poisson error model.

The ability to reject the Poisson error model in favour of the negative binomial error model increases as the number of estimated parameters is reduced (either by parameterizing the selectivity function more parsimoniously or by assuming that the population size-structure is independent of habitat type and depth zone). This result is not unexpected because considering simpler models decreases the ability of the model to fit the data, which is interpreted by the negative binomial-based analysis as sampling error

Table 3. Comparison of the fit of the full model (Ia) and those of various submodels based on the assumption that population size-structure differs among habitat types and depth zones for the five species

Results are shown for the negative binomial and Poisson ($\alpha \rightarrow \infty$) distributions. The value given in the column 'Ia' is the negative log-likelihood for model (Ia) and those in the remaining columns are the differences between the negative log-likelihood for the submodel concerned and that of model Ia, and the differences in the number of estimated parameters for sub- and full models (in parentheses). Symbols * and ** denote statistical significance at the 5 and 1% levels, respectively, based on the likelihood ratio test

	Model			
	Ia	Ib	Ic	Id
	Negative binomial error model			
Quota species				
Gummy shark	−207.46	1.54 (3)	0.42 (3)	1.87 (6)
Blue warehou	−662.20	3.74 (3)	23.45 (6)**	25.39 (9)**
Tiger flathead	−209.74	2.08 (3)	6.64 (3)**	8.56 (6)**
Jackass morwong	−1382.21	5.70 (3)**	0.10 (3)	8.19 (6)*
Non–quota species				
Dogfish	−7184.98	9.33 (6)**	11.53 (9)**	19.28 (12)**
	Poisson error model			
Quota species				
Gummy shark	−207.77	1.55 (2)	0.27 (2)	1.79 (4)
Blue warehou	−653.15	5.29 (2)**	28.77 (4)**	31.64 (6)**
Tiger flathead	−207.77	2.63 (2)	6.04 (2)**	8.42 (4)**
Jackass morwong	−1346.20	0.39 (2)	0.11 (2)	0.69 (4)
Non–quota species				
Dogfish	−7037.55	16.40 (4)**	19.51 (6)**	37.82 (8)**

over and above Poisson error. The ability to reject the Poisson error model is greater when making comparisons using the likelihood ratio test. This serves as a warning because, for several of the comparisons, neither the fit of the negative binomial model nor that of the Poisson model fits the data particularly well (as demonstrated by the values for the goodness-of-fit test).

Three of the species (blue warehou, jackass morwong and dogfish) indicate larger variability in expected catch numbers than that associated with a pure Poisson process. However, the fits to the data for these three species fail the goodness-of-fit test even for the negative binomial distribution when population structure is assumed to be habitat- and depth zone-specific. This implies that simply allowing for additional variance is insufficient to solve problems related to goodness-of-fit, and suggests instead that some of the problem may be related to model misspecification.

The issue of model selection is examined further in Table 5, which shows results for four models that examine whether selectivity and population structure are depth-specific for flathead (chosen because the fits satisfy the goodness-of-fit tests). It also examines the implications of whether data for other types of strata (habitat type in this case) should be pooled over when conducting such analyses. The results indicate that irrespective of how the data for different habitats are treated, the data cannot be pooled across depth zone. The reason that selectivity for flathead depends on depth zone is that the value of the parameter that determines the variance of the selectivity pattern (θ^2) is substantially larger for Depth Zone D. Figure 1 contrasts the selectivity patterns for the 2, 3 and 4-inch gill-nets based on data for Depth Zones B and D. Although the selectivity curves achieve their maxima at virtually the same size, those for Zone D are notably broader.

The assumption that population size-structure is independent of depth zone leads to significantly poorer fits, which is hardly unexpected given that the average size of most South East Fishery (SEF) species increases with depth (Furlani *et al.*, in press). This suggests that the implicit assumption common to most studies that selectivity is independent of environmental variables (such as depth and habitat type) is often violated.

The fits for Model Id are examined further to identify the possible cause for the failure to satisfy the goodness-of-fit tests: the values of θ_1 were estimated for each mesh size separately rather than assuming that θ_1 is the same for each mesh size. Model Id was chosen for this exercise because it is the most general model in which selectivity is assumed to be independent of habitat type and depth zone (Table 2). This assumption is needed to ensure that all of the θ_1s are estimable. The estimates of θ_1 (by mesh size) with their asymptotic 95% confidence intervals are shown for each of the five species in Fig. 2. The estimates of θ_1 for the two species that satisfy the goodness-of-fit test (gummy shark and flathead) are reasonably comparable with the

Table 4. Likelihood test probability levels and values for the χ^2 goodness-of-fit statistic for comparisons between the negative binomial and Poisson error distributions

Symbols * and ** denote statistical significance at the 5 and 1% levels, respectively

(a) Habitat and depth zone-specific population structure

Species		Likelihood ratio tests				Goodness-of-fit tests, model Ia			
		Negative binomial *v.* Poisson				Negative binomial		Poisson	
	Model:	Ia	Ib	Ic	Id	χ^2	$\chi^2_{0.05}$	χ^2	$\chi^2_{0.05}$
Quota species									
Gummy shark		0.593	0.383	0.449	0.187	57.86	108.65	67.94	112.02
Blue warehou		0.001	0.000	0.000	0.000	155.71**	104.14	195.33**	108.65
Tiger flathead		0.268	0.080	0.254	0.056	40.15	56.94	54.20	60.48
Jackass morwong		0.000	0.000	0.000	0.000	104.53*	100.75	142.53**	104.14
Non-quota species									
Dogfish		0.000	0.000	0.000	0.000	430.22**	233.99	730.12**	239.40

(b) Habitat and depth zone-independent population structure

Species		Likelihood ratio tests				Goodness-of-fit tests, model IIa			
		Negative binomial *v.* Poisson				Negative binomial		Poisson	
	Model:	IIa	IIb	IIc	IId	χ^2	$\chi^2_{0.05}$	χ^2	$\chi^2_{0.05}$
Quota species									
Gummy shark		0.000	0.000	0.000	0.000	69.74	120.99	123.92	124.34
Blue warehou		0.000	0.000	0.000	0.000	140.32*	129.92	315.58**	134.37
Tiger flathead		0.003	0.001	0.001	0.000	48.63	67.50	88.46**	70.99
Jackass morwong		0.000	0.000	0.000	0.000	127.42*	116.51	194.91**	118.75
Non-quota species									
Dogfish		0.000	0.000	0.000	0.000	317.54**	277.14	395.27**	282.51

assumption (Eqn 3) that θ_1 is independent of mesh size. For these species, the point estimate of θ_1 when this parameter is assumed to be independent of mesh size falls within most of the 95% confidence intervals for the individual θ_1s. In contrast, the estimates of θ_1 for blue warehou and dogfish exhibit clear declining trends with increasing mesh size. These species clearly violate the assumption underlying Eqn (3) that the length of fish corresponding to maximum selectivity is linearly proportional to mesh size, and so these species are not considered further in this paper.

Estimated selectivity patterns

Figure 3 shows the estimated selectivity patterns by depth zone for 3", 4" and 6" gill-nets (with their asymptotic 95% confidence intervals) for jackass morwong, tiger flathead and gummy shark. The results in Fig. 3 are based on Model Ib. Selectivity patterns for 6" gill-nets are not shown for morwong because this species was not caught using 6" gill-nets. Results are not shown for blue warehou and dogfish because the models considered in this paper were inadequate for those species.

The uncertainty about the selectivity curve for gummy shark is greater for Zone B, although the point estimates of the selectivity curves are actually quite similar (Fig. 3). The uncertainty about the flathead selectivity curves is greatest of the three species and, as noted above, the selectivity curves for Zone D are notably wider than those for Zone B. The same features are evident for morwong. There is a tendency for the 95% confidence intervals to be wider for the largest mesh size, although the reason for this is unclear.

General discussion

The problem that fits of selectivity functions to experimental data based on the assumption of a Poisson sampling process violate the assumption that the variance is equal to the mean has been identified before (Millar and Fryer 1999). However, to date, only *ad hoc* approaches have been proposed for dealing with this problem (e.g. Fryer 1991; Punt *et al.* 1996; Millar and Fryer 1999).

In contrast, the current study makes it explicit that there is variability in addition to Poisson sampling variability through the assumption that the Poisson mean is itself gamma distributed. It is straightforward to apply the generalized method for estimating selectivity when functional forms other than a gamma function, such as the logistic, normal or skewed normal functions, represent selectivity as a function of size. Although algebraically more complicated, it is also possible to represent the variation in the mean of Poisson distribution by using alternative distributions by such as the log-normal distribution.

There are clear monotonic trends in θ_1 with increasing mesh size for blue warehou and dogfish (Fig. 2). The assumption of the underlying model that the length at

Table 5. Results of likelihood ratio tests for tiger flathead to assess whether selectivity and population structure can be pooled across Depth Zones B and D

Results are shown for the data pooled across habitat types and the data are not pooled but instead catchability coefficients estimated for each combination of habitat type and depth zone

Variables independent of habitat	Negative binomial $-\ell nL$	α	P(df)	Poisson $-\ell nL$	P(df)
	Data pooled across habitat types				
Neither	–297.49	~ ∞ (B); 5.23 (D)		–293.35	
Selectivity	–290.95	8.63	0.004 (3)	–287.88	0.004 (2)
Selectivity & population structure	–283.95	3.23	0.001 (8)	–275.53	0.000 (7)
Population structure	–289.19		0.005 (5)	–279.72	0.000 (5)
	Data not pooled across habitat types				
Neither	–205.71	~ ∞ (B); 5.21 (D)		–202.13	
Selectivity	–199.22	7.64	0.005 (3)	–196.29	0.003 (2)
Selectivity & population structure	–192.18	3.48	0.000 (7)	–184.17	0.000 (6)
Population structure	–194.94		0.000 (4)	–188.76	0.000 (4)

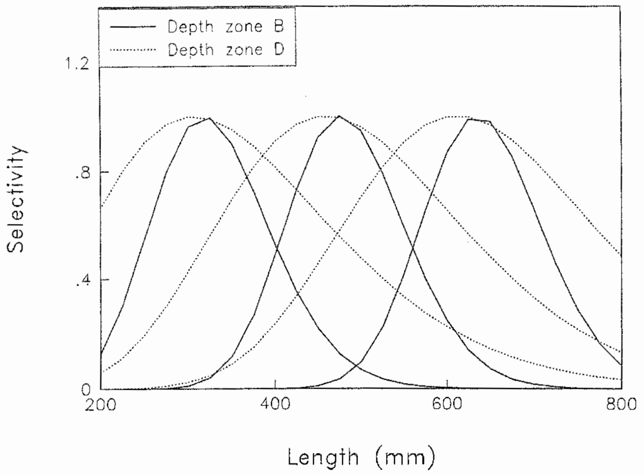


Fig. 1. Selectivity patterns for 2", 3" and 4" gill-nets for tiger flathead. Results are shown when selectivity is assumed to be a function of depth zone.

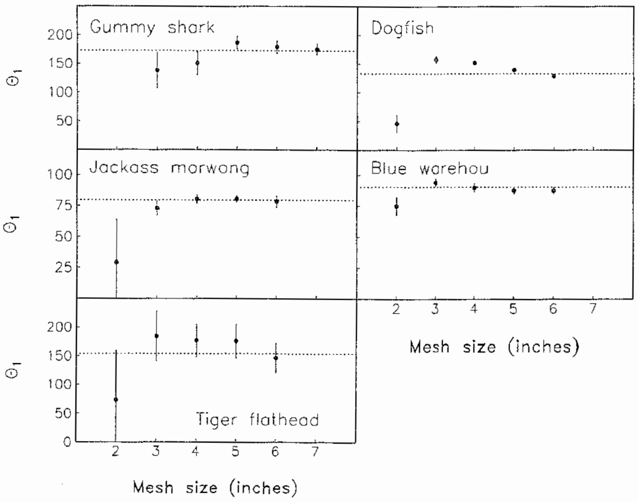


Fig. 2. Estimates, based on Model Id, of θ_I by mesh size (with asymptotic 95% confidence intervals) for each of the five species. The dotted lines indicate the values for θ_I when this parameter is assumed to be independent of mesh size.

maximum selectivity is linearly proportional to mesh size is clearly violated for these species. Ideally, a fish coming into contact with a gill-net is caught when the mesh is large enough to let the head through past the gillcovers, but not so large that the fish can pass all the way through. This process can be represented by growth in length when growth is isometric so that body girth increases proportionally with fish length. However, if growth in girth is not isometric or the fish is compressible and can distort its shape to escape the mesh, then an alternative model relating fish size to selection may be required (Santos *et al.* 1995).

The study also shows that there is considerable difficulty in estimating selectivity in complex environments such as the SEF. There are many biological and environmental factors that differentially affect different sizes of fish. For example, of 50 species sampled in numbers on the south-east Australian shelf, 27, including 12 quota species, showed distinct changes in size composition with depth (Furlani *et al.*, in press). These 27 species could be separated into four distinct groups, which, in some instances, have different size compositions between sandy and rocky habitats. Failing to account for this and other distributional variability will compromise any selectivity estimates determined from aggregated data.

The analyses could not have been performed had the experiment been conducted in only a single area (and hence depth zone/habitat type). Any resulting selectivity pattern from a single area study would, almost certainly, have been assumed common to all areas in the fishery. It is clear, therefore, that the default option when designing experiments for estimating gill-net selectivity should be that

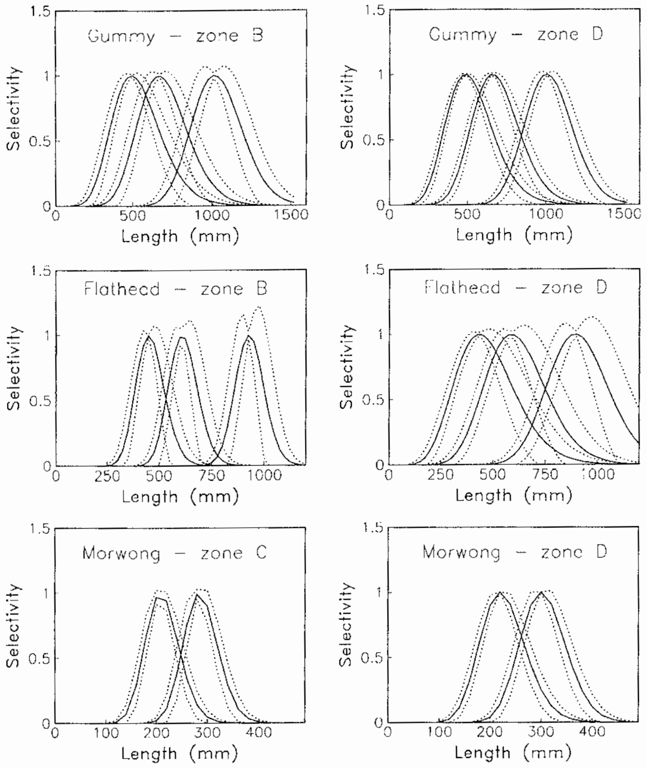


Fig. 3. Selectivity patterns for 3", 4" and 6" gill-nets based on fits of Model Ib. The dotted lines represent asymptotic 95% confidence intervals. Results are shown for two depth zones for three of the five species.

selectivity depends on (at least) depth and habitat type. Considerable care needs to be taken when designing future experiments. For example, where estimates of selectivity patterns are to be used in stock assessments, experiments should be conducted primarily in depth zones/habitat types in which the bulk of the catch is taken. Furthermore, stock assessments may need to disaggregate catches by depth zone/habitat type if size structure/selectivity differs among these strata. There is also a need to carefully record and understand the behaviour of species included in future selectivity-related experiments.

The estimates of θ_1 for 2$''$ mesh are anomalous for four of the five species (being the lowest for any mesh size; Fig. 2). The exact reasons for this result remain unknown but it may be that the processes that lead to capture in 2$''$ gill-nets are quite different from those for larger mesh sizes. Field observations indicate that fish caught in smaller mesh gill-nets are often tangled by spines or teeth (A. Williams, CSIRO Marine Research, personal communication). This was especially evident in the spiny dogfish a species that was observed to get entangled by its dorsal spine and then roll up in loose mesh. Some authors (e.g. Mattson 1994) have noticed the problem of entanglement in small mesh gill-nets but concluded that this would not influence overall selectivity estimates. Other authors (e.g. Anderson 1998; Hovgård *et al.* 1999) highlight the need to consider the capture process in gill-nets explicitly when estimating selectivity. Future selectivity-related work in the SEF should consider attempting to partition selectivity into its different constituent processes and then developing models for each process.

The study has examined the data for each species separately and assessed whether the selectivity and/or population size-structure differs among depth zones/habitat types. However, there is no reason that future work could not examine, for example, whether selectivity can be parameterized so that some of the model parameters are common across species. The results of such analyses could then be used to provide information on selectivity patterns for those species for which the data collected during the current experiment were insufficient to estimate selectivity.

Acknowledgments

It is a pleasure to acknowledge the assistance of Alan Williams (CSIRO Marine Research) who led the project that collected the data used in this paper, the skippers of FV *Starfire* (Horst Fischer and Nick Albers) and FV *Erin Jay* (Kevin Haslam), their crews, and the scientists on board: Bruce Barker, Neil Klaer, Tim Lamb, Mark Lewis and Mark Green (CSIRO). Tony Smith and Beth Fulton (CSIRO Marine Research) are thanked for their comments on an earlier version of this paper.

References

Anderson, C. S. (1998). Partitioning total size selectivity of gill nets for walleye (*Stizostedion vitreum*) into encounter, contact and retention components. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1854–63.

Augustin, N. H., Borchers, D. L., Clarke, E. D., Buckland, S. T., and Walsh, M. (1998). Spatiotemporal modeling for the annual egg production method of stock assessment using generalized additive models. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2608–21.

Cui, G., Williams, B. J., and Kuczera, G. (1999). A stochastic Tokunaga model for stream networks. *Water Resource Research* **35**, 3131–42.

Fryer, R. J. (1991). A model of between-haul variation in selectivity. *ICES Journal of Marine Science* **48**, 281–90.

Furlani, D., Williams, A., and Bax, N. (in press). Fish Biology. In 'Habitat and Fisheries Production in the South East Fishery Ecosystem. Final Report to FRDC'. (Eds N. Bax and A. Williams.) pp. 00–00. (CSIRO Marine Research: Hobart.)

Gomon M. F., Glover J. C. M., and Kuiter, R. H. (1994). The fishes of Australia's south coast. (State Printer: Adelaide.)

Hamley, J. M. (1975). Review of gillnet selectivity. *Journal of the Fisheries Research Board of Canada* **32**, 1943–69.

Henderson, B. A., and Wong, J. L. (1991). A method for estimating gillnet selectivity of walleye (*Stizostedion vitreum vitreum*) in multimesh multifilament gill nets in Lake Erie, and its application. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 2420–28.

Hovgård, H., Lassen, H., Madsen, N., Moth Poulsen, T., and Wileman, D. (1999). Gillnet selectivity for North Sea Atlantic cod (*Gadus* *morhua*): model ambiguity and data quality are related. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1307–16.

Johnson, N. J., and Kotz, S. (1969). Discrete distributions. (Houghton Mifflin: Boston.)

Kirkwood, G. P., and Walker, T. I. (1986). Gill net mesh selectivities for gummy shark, *Mustelus antarcticus* Günther, taken in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **37**, 689–97.

Last, P. R., and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' (CSIRO: Melbourne.)

Marchal, P., and Horwood, J. (1996). Long-term targets for the Celtic Sea mixed-species multi-métiers fisheries. *Aquatic Living Resources* **9**, 81–94.

Mattson, N. S. (1994). Direct estimates of multi-mesh gillnet selectivity to *Oreochromis shiranus chilwae*. *Journal of Fish Biology* **45**, 997–1012.

Millar, R. B., and Fryer, R. J. (1999). Estimating the size-selection curves of towed gears, traps, nets and hooks. *Reviews in Fish Biology and Fisheries* **9**, 89–116.

Millar, R. B., and Walsh, S. J. (1992). Analysis of trawl selectivity studies with an application to trouser trawls. *Fisheries Research* **13**, 205–20.

McConnell, H., and Horn, J. M. (1972). Probability of surface karst. In 'Spatial Analysis in Geomorphology'. (Ed. R. J. Choley.) pp. 164–75. (Methuen: London.)

Mood, A. M., Graybill, F. A., and Boes, D. C. (1974). 'Introduction to the Theory of Statistics.' 3rd Edn. (McGraw-Hill: Singapore.)

Murawski, S. A. (1984). Mixed-species yield-per-recruitment analyses accounting for technological interactions. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 897–916.

Murawski, S. A. (1996). Factors influencing by-catch and discard rates: analyses from multispecies/multifishery sea sampling. *Journal of Northwest Atlantic Fisheries Sciences* **19**, 31–9.

Perez-Comas, J. A., Erickson, D. L., and Pikitch, E. K. (1998). Cod-end mesh size selection for rockfish and flatfish of the US West Coast. *Fisheries Research* **34**, 247–68.

Pierce, R. B., Tomcko, C. M., and Kolander, T. D. (1994). Indirect and direct estimates of gill-net selectivity for northern pike. *North American Journal of Fisheries Management* **14**, 170–77.

Pikitch, E. K. (1987). Use of a mixed-species yield-per-recruit model to explore the consequences of various management policies for the Oregon flatfish fishery. *Canadian Journal of Fisheries and Aquatic Sciences* **44** (Suppl. 2), 349–59.

Punt, A. E., and Walker, T. I. (1998). Stock assessment and risk analysis for the school shark (*Galeorhinus galeus*) off southern Australia. *Marine and Freshwater Research* **48**, 719–31.

Punt, A. E., Pulfrich, A., Butterworth, D. S., and Penney, A. J. (1996). The effect of hook size on the size-specific selectivity of hottentot *Pachymetopon blochii* (Val.), and its effects on yield per recruit computation. *South African Journal of Marine Science* **17**, 155–72.

Regier, H. A., and Robson, D. S. (1966). Selectivity of gill nets, especially to lake whitefish. *Journal of the Fisheries Research Board of Canada* **23**, 423–54.

Sainsbury, K. J. (1984). Optimal mesh size for tropical multispecies fisheries. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **41**, 129–39.

Santos, M. N., Monteiro, C. C., and Erzini, K. (1995). Aspects of the biology and gillnet selectivity of the axillary seabream (*Pagellus arcane*, Risso) and the common pandora (*Pagellus erythrinus, Linnaeus*) from the Algarve (south Portugal). *Fisheries Research* **23**, 223–36.

Walker, T. I. (1992). A fishery simulation model for sharks applied to the gummy shark, *Mustelus antarcticus* Günther, from southern Australian waters. *Australian Journal of Marine and Freshwater Research* **43**, 195–212.

Welch, D. W., and Ishida, Y. (1993). On the statistical distribution of salmon in the sea: application of the negative binomial distribution, and the influence of sampling effort. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1029–38.

Williams, A., and Bax, N. J. (2001). Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52**, 513–36.

Manuscript received 10 November 1999; revised and accepted 21 July 2000

Mar. Freshwater Res., 2001, **52**, 701–17

Stock assessment of the blue grenadier *Macruronus novaezelandiae* resource off south-eastern Australia

A. E. Punt[AD], *D. C. Smith*[B], *R. B. Thomson*[A], *M. Haddon*[C], *X. He*[A] *and J. M. Lyle*[C]

[A]CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia
[B]Marine and Freshwater Resources Institute, Department of Natural Resources and Environment, PO Box 114, Queenscliff, Vic. 3225, Australia
[C]Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, GPO Box 252-49, Hobart, Tas. 7001, Australia
[D]Contact address: School of Aquatic and Fisheries Sciences, Box 355020, University of Washington, Seattle, WA 98195-5020, USA

Abstract. The fishery can be divided into two subfisheries ('spawning' and 'non-spawning'). Commercial catch rates for the 'non-spawning' subfishery declined from the late 1980s to 1997, whereas those for the 'spawning' subfishery exhibit no obvious temporal trend. An 'Integrated Analysis' assessment, of the feasibility of reconciling these differing trends, uses catch (landed and discarded), catch rate, length-at-age, and catch-at-age data and estimates of absolute abundance based on the egg-production method. It emphasizes uncertainty due to model assumptions and the data included in the assessment. Use of the discard data allows more precise estimation of the magnitude of recent recruitments. Spawning biomass is estimated to have declined from a peak in 1989–91 to 1999 although fishing mortality has consistently been <6% for each subfishery. One main reason for the reduction in population size is the weakness of year-classes spawned from 1988 to 1993. Differences in catch rates between the two subfisheries can therefore be explained by interactions between the components of the population harvested by the two 'subfisheries', and the trends in year-class strength. A risk analysis is used to evaluate the consequences of different future levels of harvest for different assessment assumptions. Overall, the spawning biomass is predicted to increase over the next five to ten years as a result of the strong 1994 and 1995 year-classes, although the extent of this increase remains uncertain.

Introduction

In Australian waters, blue grenadier (*Macruronus novaezelandiae*) are found from mid New South Wales to southern Western Australia, including the coasts of Tasmania and across the Great Australian Bight (Smith 1994). Blue grenadier are also found in New Zealand and support a very large fishery there. The available data (Milton and Shaklee 1987; Gunn *et al.* 1989; Thresher *et al.* 1989) do not provide evidence for multiple stocks in Australian waters, although electrophoretic data (Milton and Shaklee 1987) indicate significant differences between the stocks of blue grenadier in Australia and those in New Zealand.

Although the bulk of the catch is taken by demersal and mid-water trawl, as is the case for most of the species in the South East Fishery (SEF), blue grenadier are caught with many gear types across a wide geographic range. The fishery can be divided for statistical and assessment purposes into two subfisheries: a 'spawning' subfishery that operates on the spawning stock in winter (June, July and August) off western Tasmania (Fig. 1), and a 'non-spawning' subfishery that includes all other catches in the SEF. Catches by the 'non-spawning' subfishery primarily comprise sub-adult and small adult fish, whereas the 'spawning' subfishery concentrates on mature fish, including large adults that are poorly represented in the catches by the 'non-spawning' subfishery (Smith 1998*a*). The proportion of the total catch taken in the 'spawning' subfishery has varied around a mean of 37% of the total from 1986 to 1991 and then increased steadily to a maximum of about 73% in 1997 (Fig. 2).

Catches of blue grenadier were negligible until the trawl fleet began to exploit the deeper waters off western Victoria and Tasmania in the late 1970s. At present, the catch of blue grenadier is the largest of all of the species in the South East Fishery in weight and second largest in terms of value (e.g. $A8.8m in 1998). Most blue grenadier are taken between 300 and 600 m with a peak in catches occurring in the 450–550 m depth range (Smith 1994, 1998*a*). The fishery for blue grenadier has been managed with output controls implemented as Individual Transferable Quotas since 1992.

10.1071/MF99136 1323-1650/01/040701

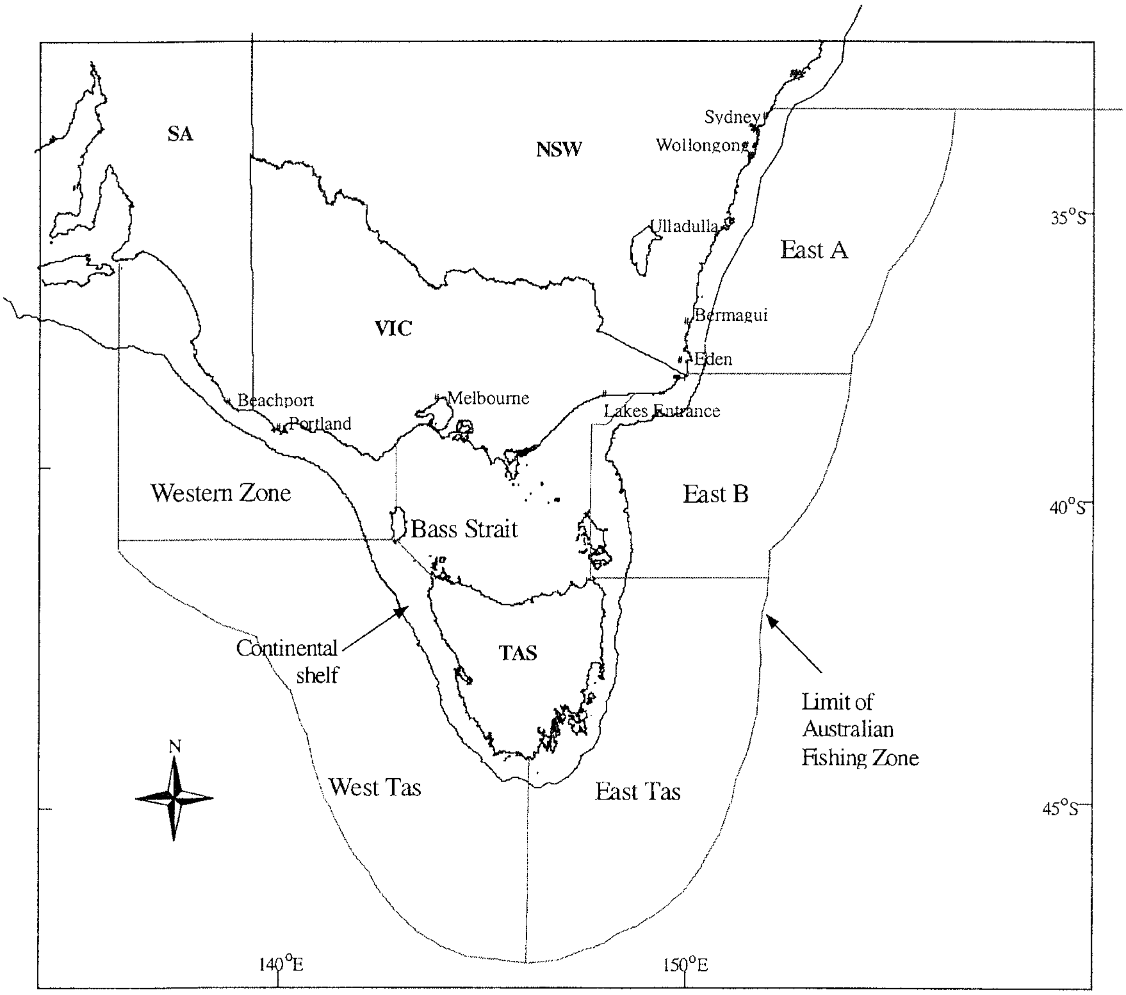


Fig. 1. Map of southern Australia showing the areas mentioned in the text.

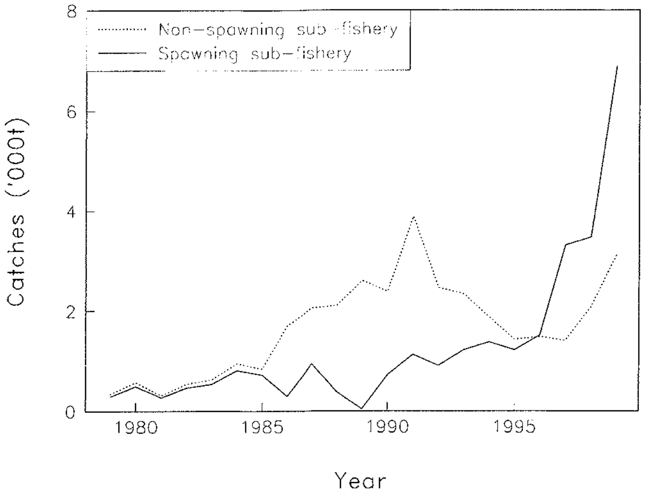


Fig. 2. Landed catches of blue grenadier (1979–99) by the 'spawning' and 'non-spawning' subfisheries.

The initial Total Allowable Catch, TAC, was 5000 t. This was increased to 10000 t in 1994 and has remained at 10000 t ever since, although the 10000 t TAC was only reached in 1999.

Catch rates in the 'non-spawning' subfishery declined almost continuously from 1990 to 1997 (Fig. 3), a period when catches in the 'spawning' subfishery increased by over 300%. This led to concern amongst some fishers who operate primarily in the 'non-spawning' subfishery that the TAC for the fishery was too high and that their reduced catches were a consequence of overexploitation by, or competition with, the 'spawning' subfishery. This view was in stark contrast to that of fishers who operate primarily in the 'spawning' subfishery whose catch rates have been variable but do not exhibit any obvious temporal trend (Fig. 3).

The differences in catch rate trends between subfisheries led to antagonism between the fishers in the two subfisheries. Additionally, some fishers in the 'non-

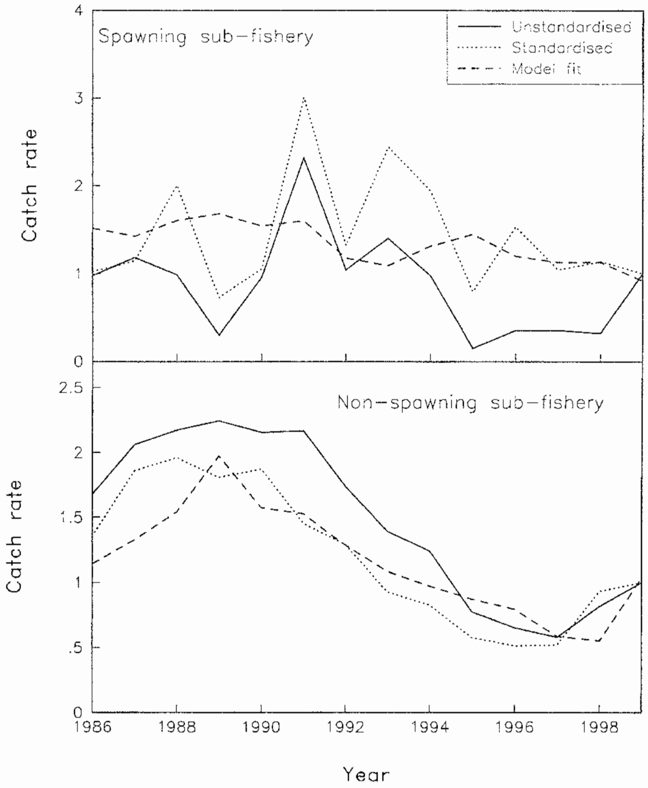


Fig. 3. Catch rate indices for the 'spawning' and 'non-spawning' subfisheries. Solid lines, unstandardized (geometric mean) catch rates; dotted lines, standardized catch rates; dashed lines, base-case model predictions corresponding to the mode of the posterior distribution.

spawning' subfishery began to lose faith in the scientists involved in the assessment process because, using biomass estimates from the egg production method (Bulman *et al.* 1999), the assessment biologists concluded that the resource was relatively unexploited and that TACs could, in fact, be increased (rather than decreased as was being argued by some at the time). The early assessments considered the data for the two subfisheries separately. Therefore, it was not possible to determine whether this was a case in which catch rates for one of the subfisheries were not indexing abundance adequately or whether the catch rate trends for the two subfisheries were actually consistent given that they operate on different components of the population. At the same time that the disagreements among the subfisheries were at their greatest, an on-board monitoring programme and comments by fishers indicated very large-scale discarding of small fish by the 'non-spawning' subfishery.

To address the above issues, a multi-fleet stock assessment model based on the 'Integrated Analysis' approach (Fournier and Archibald 1982; Methot 1989, 1990) was developed. This model was then used as the basis for a quantitative analysis of whether the catch rate data for the two subfisheries could be reconciled or whether it was necessary to conduct assessments based on each catch rate series separately and report such results to management, as is common when dealing with conflicting data sources (Richards 1991; Punt and Hilborn 1997). Unlike most other assessments based on 'Integrated Analysis', the current assessment makes use of the information collected from the discards (fraction of the catch discarded and its age-structure) to 'index' the sizes of the year-classes that are about to enter the fishery. This is important because uncertainty about future recruitment is key when conducting risk analyses to consider, for example, the biological effect of future catch limits. Unlike other fisheries jurisdictions, such as the European Union, stock assessments in Australia emphasize consideration of uncertainty (Smith *et al.* 2001; Punt *et al.* 2001). This paper therefore examines model sensitivity by changing some of the assumptions of the assessment, and by representing uncertainty through Bayesian posterior distributions (Punt and Hilborn 1997).

Materials and methods

Assessment model

The assessment is based on an age- and sex-structured population dynamics model that recognizes the 'spawning' and 'non-spawning' subfisheries (Appendix A). The model treats landed and discarded catches separately. It explicitly considers the processes that lead to discarding by forcing the rate of discarding to depend on length and to be density-dependent (i.e. the rate of discarding is greater for larger year-classes). Density-dependent discarding is to be expected in this fishery because, although it is possible to market some small fish, when very large cohorts enter the fishery, high-grading (and hence discarding) will occur. Even though most of the assessment data are sex-aggregated, it is necessary for the model to be sex-structured because the estimates of abundance from the annual egg production method relate only to females and the rate of natural mortality for males is greater than that for females.

Fishing mortality is assumed to be 'separable' by subfishery, i.e. for each subfishery it is assumed that fishing mortality-at-age can be expressed as the product of an age-specific (vulnerability) and a year-specific (annual fully selected fishing mortality) component. Length- and mass-at-age are permitted to vary over time. They are estimated from the age–length keys, the length–frequency distributions and the relationship between mass and length (Method 2 of Punt and Smith 2001).

Data used

Six sources of data are taken into account in the assessment: catch in mass, information on discards, catch rate indices, catch age-composition data, length-at-age information from age–length keys, and egg production estimates. Each of these sources of information will be considered in turn.

Catches (landed and discarded)

Unlike the case for most other SEF species, catches are available for essentially the entire period of exploitation (Fig. 2). Prior to 1984, however, logbook coverage of the fishery was voluntary so the catches for these years are incomplete. However, given the magnitude of the reported catches, it seems unlikely that even fairly extensive errors in catch estimation prior to 1984 will affect the qualitative (and even quantitative) results of any assessment of blue grenadier. In certain circumstances, blue grenadier are headed and gutted at sea. Separate factors for the 'non-spawning' and 'spawning' subfisheries (1.4 and

1.2 respectively (Chesson and Staples 1995)) are used to convert landed catches from processed to whole weight. The lower factor for the 'spawning' subfishery reflects a higher proportion of the catch landed whole.

The magnitude of the catch discarded annually by the 'non-spawning' subfishery has been estimated based on commercial catch sampling programmes since 1995. Discard rates (discarded/total catch) were estimated separately for the east (east of 147° East) and the west (west of 147° East) of the fishery, and an overall discard rate determined after accounting for the relative magnitude of the catches in the east and in the west. On-board monitoring indicated substantially increased discard rates in 1996 that have continued through 1998. By weight, 48, 79 and 47% of the catch was discarded in 1996, 1997 and 1998, respectively, in the 'non-spawning' subfishery. Discarding of small fish in the 'spawning' subfishery is essentially non-existent because small fish are virtually absent from the catches. However, the catches for the 'spawning' subfishery used in the assessment include anecdotal estimates of the mass of fish caught but not landed because of, for example, burst trawl nets. The effect of this was estimated by fishers to be greatest in 1993 (25% of the catch lost) but is currently <10%.

Catch rate indices (indices of relative abundance)

Standardized catch rate indices were based on data for vessels that had been active in the fishery for at least two years and caught at least 5 t of blue grenadier per year. General Linear Models, based on a variety of factors, were fitted to the catch and effort data (defined as kg landed whole weight and hours fished, respectively) under the assumption that the logarithm of the catch rate is normally distributed, as is common practice (Vignaux 1993; Klaer 1994). The main factors considered were year, vessel, week, catch of pink ling, and depth category, but depth category–week and depth category–vessel interactions were also examined. The factor 'week' was defined as the date in days from the start of year divided by seven. The depth of the trawl was divided into 50 m categories from 50 to 1250 m and the catch of pink ling was divided into five categories (<100 kg, <200 kg, <500 kg, <1000 kg and >1000 kg). Models were fitted separately to data for the 'spawning' and 'non-spawning' subfisheries.

The most appropriate model to describe the catch and effort data was selected according to the Akaike Information Criterion (Burnham and Anderson 1998). For both subfisheries, the model selected included all four of the main factors but none of the interaction terms. This statistical model explained 57.6% and 35.3% of the variance in catch rate for the 'spawning' and 'non-spawning' subfisheries respectively. Compared with the unstandardized (geometric mean) catch rates, the standardized catch rate series for the 'non-spawning' subfishery declines to a lesser extent, whereas that for the 'spawning' subfishery is less variable (Fig. 3).

The procedure used to standardize the catch-and-effort data should remove the effect of the factors considered. However, there are many other factors that influence the relationship between abundance and catch rate, such as changes in fishing practices, and improvements over time in technology. In particular, the 'spawning' fishery is based on identifying schools and then fishing them, which may lead to hyperstability of catch rates, whereas the 'non-spawning' fishery is part of a multispecies complex in which 'targeted effort' may, in actuality, have little meaning. Information about these factors (and their magnitude) is not available so, in addition to the base case assumption that catch rate is linearly proportional to abundance, sensitivity is also explored to the alternative assumption that it is proportional to the square root of abundance (after Cooke and Beddington 1984; Butterworth and Punt 1992). Sensitivity is also explored to ignoring the catch rate data altogether and to basing the assessment on one but not both catch rate indices.

Age- and size-composition data

The age- and size-composition of the catch differs markedly between the 'spawning' and 'non-spawning' subfisheries. The basic data on the age- and size-composition of the catch were obtained from the State agencies of Victoria (Smith 1998*b*) and Tasmania (Lyle, unpublished), and more recently from the Integrated Scientific Monitoring Program (Knuckey *et al.* 1999). Information on the size-composition of the catch by the 'spawning' subfishery was first collected in 1984 and 1985, then again in 1988, and each year since 1991. Size-composition information was first collected from the 'non-spawning' subfishery in 1987 and 1988, and size-composition data were collected each year from 1990. Where commercial catches are headed and gutted at sea, the agencies responsible have adjusted the catches by use of conversion factors as appropriate (e.g. Smith *et al.* 1995).

Ageing of blue grenadier is based on the counting of annuli in sectioned otoliths at the Central Ageing Facility (Morison *et al.* 1998). Validation of the ageing technique has been achieved by the bomb radiocarbon method (Kalish *et al.* 1997) and the progression of cohorts through the catches over a period of more than a decade (Fig. 4). Replicate counts of the same otoliths show moderately high levels of variability between readers and by the same reader (Smith *et al.* 1995; Table A.1), so one of the sensitivity tests examines the effect of ageing error when fitting to the age-composition data (see Eqn A.14). Estimates of the age-composition of the discarded component of the catch are available from the results of the application of age–length keys to the discard length–frequencies collected as part of on-board monitoring programmes. Because growth of blue grenadier appears to vary over time (possibly as a function of cohort size), mean length- and mass-at-age by cohort have been derived from the age–length keys, the mass–length relationship and the length–frequency data (Method 2 of Punt and Smith 2001). Sensitivity is also examined to assuming that growth follows a time- and cohort-invariant von Bertalanffy growth equation (Method 1 of Punt and Smith 2001).

Estimates of absolute abundance

Two estimates of the abundance of the spawning stock are available based on the annual egg production method (Bulman *et al.* 1999). These estimates relate to only the female component of the spawning stock because of uncertainties surrounding the sex ratios of spawning blue grenadier (Smith 1998*a*). In principle, the estimates (59 080 t (CV 0.189) and 44 195 t (CV 0.287) for 1994 and 1995, respectively) relate to the absolute abundance of females that spawned in those years. Although this is the most plausible hypothesis, considerable uncertainty exists regarding the distribution of spawning effort and fecundity across the spawning season (Bulman *et al.* 1999). Consequently, sensitivity is considered to the possibility that the estimates may be positively, or negatively, biased by 50% and 100% respectively. The sensitivity of the results to ignoring these estimates altogether is also examined. It is known from data from New Zealand (Livingston *et al.* 1997) that not all blue grenadier spawn annually. Assessments in New Zealand (e.g. McAllister *et al.* 1994) are based on the assumption that 77% (the average of the range of 68–85% reported by Livingston *et al.* 1997) of the potential spawners spawn each year. The same assumption is made here.

Parameter estimation

The maximum age, x, is taken to be 20 years, the extent of variation in year-class strength, σ_r, is taken to be 1, and steepness, h, is assumed to be 0.9. Natural mortality for males is assumed to be 120% of that for females and the natural mortality rate for females is constrained to lie

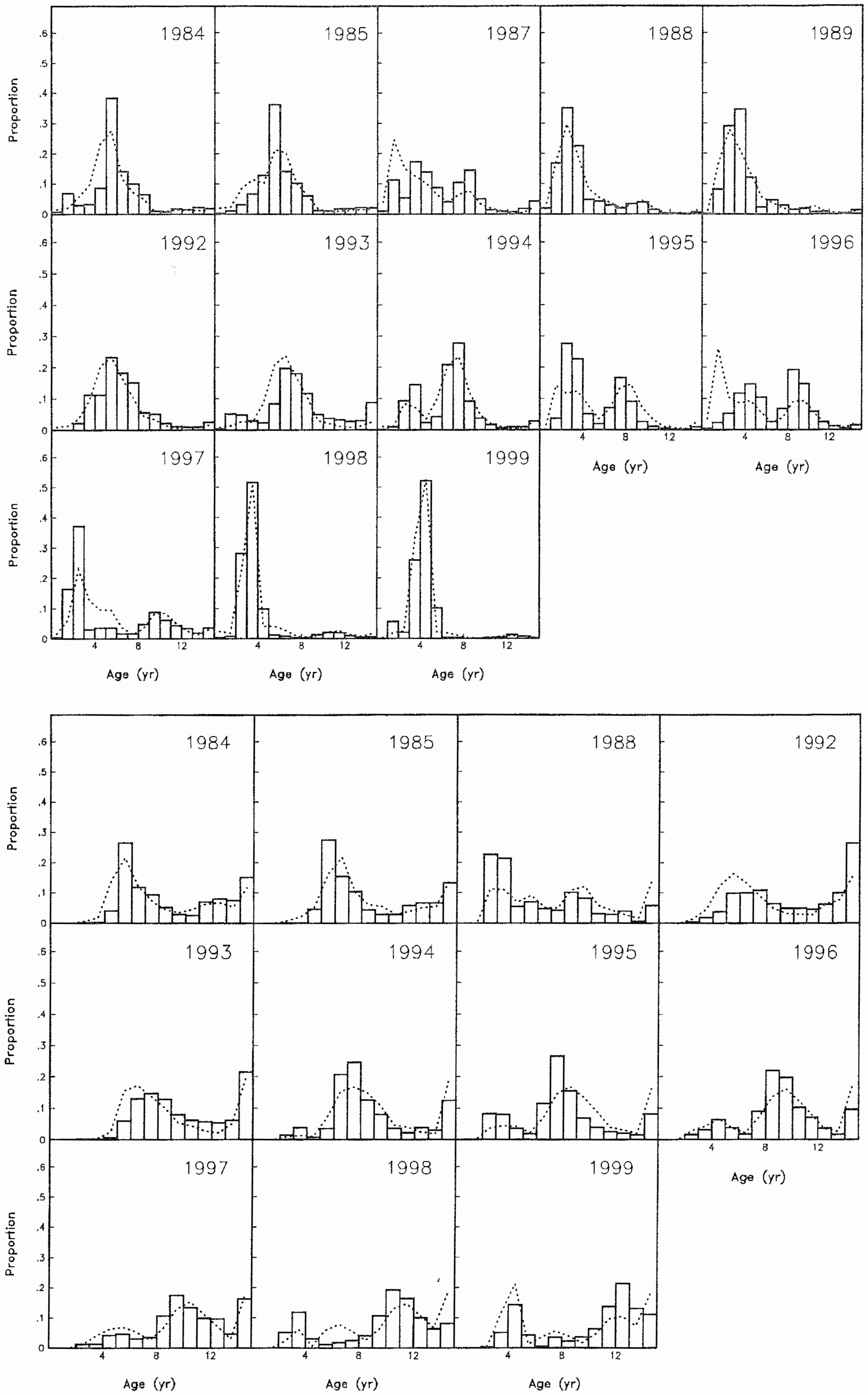


Fig. 4. Catch age-composition data for blue grenadier: *(upper)* for the 'non-spawning' subfishery and *(lower)* for the 'spawning' subfishery. Columns: observed data (based on age–length keys and length-frequencies). Dotted lines: base-case model predictions corresponding to the mode of the posterior distribution.

between 0.2 and 0.3 year^{-1}. These choices and the values assumed for x, σ_r and h are based on selections made in New Zealand (e.g. McAllister *et al.* 1994; Ballara *et al.* 1997). The selection of $x = 20$ is largely arbitrary because the age-composition data are pooled at age 15 years (see Eqn A.13 and associated discussion); essentially identical results would have been obtained for any value for x of 15 and greater.

The base-case weight, N, assigned to the age-composition data (landed and discarded; Eqn A.13) is 50[1]. The base-case choices for the residual standard deviations σ_c (landed and discarded catches; Eqn A.12) and σ_q ('spawning' and 'non-spawning' catch rate series; Eqn A.15) are taken to be 0.05, 0.3, 0.3 and 0.3 respectively. The choice $\sigma_c = 0.05$ reflects the assumption that the landed catch (in mass) is measured with considerable accuracy. The sensitivity of the results is explored to different choices for N and σ_q. The choice of σ_c for the discarded catch reflects the fact that the estimates of discards are based on sampling a subset of the fleet and is therefore subject to much more uncertainty than the landed catches.

The values for the 'free' parameters of the population dynamics model (Table 1) that maximize the likelihood function are determined with the AD Model Builder package (Otter Research Ltd 1994). The posterior distributions for the quantities of interest are determined with the Markov Chain Monte Carlo (MCMC) algorithm (Hastings 1970; Gelman *et al.* 1995; Punt and Hilborn 1997). The results in this paper are based on the results of 2000 draws from the posterior distribution. The total number of cycles was 3500000, of which the results from the first 500000 were ignored as this is a 'burn in' period to allow the algorithm to set itself up.

Table 1. The 94 estimable parameters of the population dynamics model

Parameter	Description	Number of parameters
R_0	Average year-class strength at the virgin level	1
M	Natural mortality	1
q	Catchability	2
F_y^f	Fully selected fishery mortality	42
$\varepsilon_y, \varepsilon_a$	Recruitment residuals	39
$S_{y,a}^f$	Vulnerability (landed and discarded catches)	9

Uniform priors (bounded by zero as appropriate) are selected for all of the parameters for the Bayesian analyses, except for the recruitment residuals (ε_a and ε_y in the appendix), which are assumed to be normally distributed with mean 0 and standard deviation σ_r. The uniform priors are chosen to reflect a lack of prior information. It should be noted, of course, that truly non-informative priors do not (and cannot) exist because a 'non-informative' prior for one quantity may lead to a highly informative induced prior for another quantity (Punt and Hilborn 1997).

Risk analysis

The risk analysis involves projecting the population dynamics model forward for 20 years for a variety of situations and choices for the level of catch by the 'spawning' and 'non-spawning' subfisheries. The split of the catch between these subfisheries is taken to be 75:25. The risk analysis involves selecting 2000 sets of parameter values at random from the posterior distribution and conducting a projection for each. In this calculation, variation in year-class strength is accounted for by generating a value for ε_y from $N(0;\sigma_r^2)$. The risk associated with different levels of future TAC is quantified by the probability of the (female) spawning biomass dropping below 40% and 20% of the virgin female spawning biomass, B_0. These performance measures were developed by the assessment group responsible for the blue grenadier fishery, in discussion with Australian Fisheries Management Authority and its Management Advisory Committees. Following advice from the fishing industry, the projections are based on the assumption that future TACs, which relate to landed catches only, will be taken exactly. The projections are based on assuming that future discarding by the 'non-spawning' fishery will follow the model described in the appendix.

The projections are based on fixed levels of TAC and hence should over-estimate risk because such projections implicitly assume that future data will be ignored. A more realistic, but computationally intensive, approach would be to consider feedback-control harvest strategies (e.g. Butterworth *et al.* 1997; Smith *et al.* 1999; Punt *et al.* 2001). However, consideration of such strategies is beyond the scope of this paper.

Results and Discussion

Inferences from the raw data

The observed age-composition data (Fig. 4) indicate that the 1989 year-class was particularly poor, whereas the 1994 and 1995 year-classes (4- and 5-year-olds in 1999) were very strong. The catch age-composition data for the 'non-spawning' subfishery for 1999 exhibits two modes – one corresponding to the 1994 and 1995 year-classes and another corresponding to the relatively strong 1984, 1985, 1986 and 1987 year-classes (Fig. 4*upper*). The high proportion of 15+ animals in the 'spawning' subfishery from 1984 to *c.* 1994 (Fig. 4*lower*) is notable and indicates the relatively lightly fished nature of the resource. The standardized catch rates for the 'non-spawning' subfishery (Fig. 3) confirm industry observations that substantial reductions in the biomass available to this subfishery occurred recently, whereas those for the 'spawning' subfishery show little trend.

Base-case analysis

The fit of the model to the landed catches is virtually perfect, which is not surprising given the low value assumed for σ_c. In contrast, the fit to the discards, although capturing the overall trend, is nevertheless quite imprecise (the CV of the residuals at the posterior mode is 0.69). The fits to the age-composition data are adequate in that the model is generally able to follow the patterns of strong and weak year-classes (Fig. 4). In particular, the model is able to fit the two periods of above average year-classes and the period (1988–93) of below average year-classes. Although the fits to the age-composition data are generally good, there are some cases in which the model fits very poorly. The fits to the catch rate data for the 'spawning' and 'non-spawning' subfisheries (Fig. 3), although mimicking the overall

---

[1] This choice for N is based on the approach advocated by McAllister and Ianelli (1997).

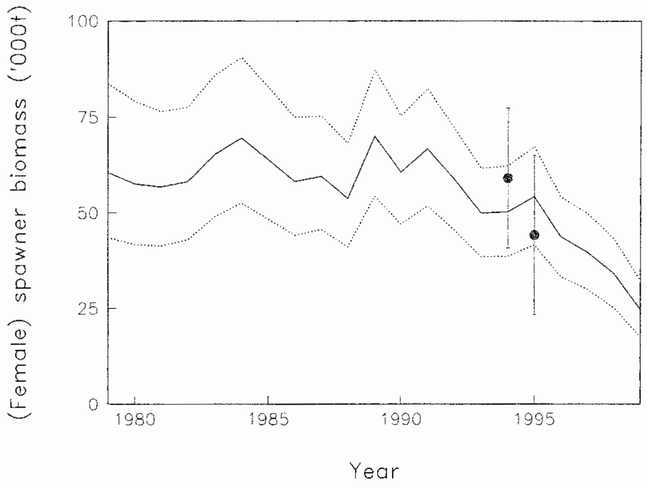


Fig. 5. Time-trajectory (posterior medians and 90% intervals) of spawner biomass (females) from the base-case analysis. ●, egg production estimates for 1994 and 1995 (with 90% CIs).

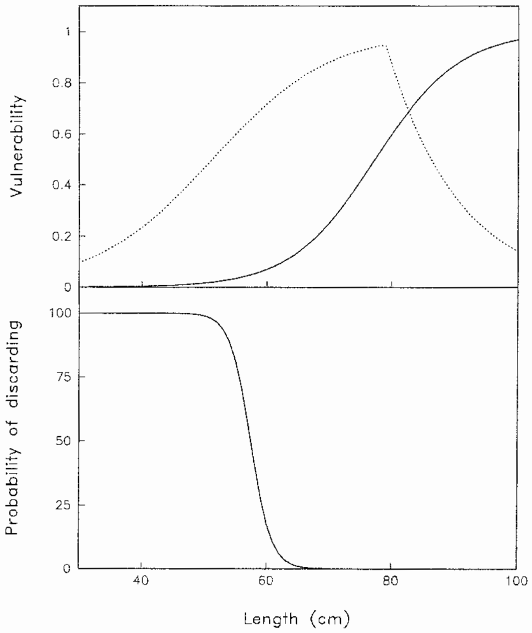


Fig. 6. Vulnerability against length by subfishery, and the probability of being discarded against length for the largest cohort in the fishery. The results in this figure pertain to the base-case analysis. Dotted line: non-spawning fishery. Solid line: spawning fishery.

Fig. 7. Time-trajectories (posterior medians and 90% intervals) of year-class strength from the base-case analysis.

patterns, are also fairly imprecise. The model is able to match the estimates of female spawner biomass from the egg production method well (Fig. 5).

The model indicates that the 'spawning' and 'non-spawning' subfisheries have notably different vulnerability patterns (Fig. 6) and that vulnerability drops off with length for the 'non-spawning' subfishery. The vulnerability pattern for the 'spawning' subfishery increases quite slowly with length, which is perhaps surprising as it implies that many fish capable of spawning are not available to the 'spawning' subfishery. However, the length-at-50%-vulnerability of 77 cm is close to the assumed length-at-maturity of 70 cm. The relatively high vulnerability of small fish is a consequence of the model attempting to fit the catch age-composition data for years (e.g. 1988 and 1995) during which substantial numbers of young fish were taken by the 'spawning' subfishery (Fig. 4 *lower*). It is known that the size of fish on the spawning grounds changes over the spawning season. Age-compositions such as those for 1988 and 1995 could arise if the fishery was concentrated near the end of the year when fish tend to be smaller than at the start. As expected, the probability of discarding is relatively high for small fish (approximately ages 1–4) but is virtually zero above 60 cm (Fig. 6). This result indicates that relatively high levels of discarding will take place when large year-classes enter the population if current fishing practices are maintained. Density-dependent discarding, although plausible, is estimated to be relatively unimportant (the point estimate of the parameter ϕ for the base-case analysis is only 0.0786).

The spawning biomass is estimated to have declined from a peak in 1989–91 to 1999 (Fig. 5), although the levels of fishing mortality have consistently been less than 6% for each subfishery. However, it should be noted that the biomass was larger than (deterministic) B_0 until 1996. This last result is not particularly surprising because the expected unfished biomass is ~65% larger than the deterministic unfished biomass[2], given the log-normal model assumed for recruitment variability and the choice $\sigma_r = 1$. One of the main reasons for the reduction in spawning biomass after 1993 was that the 1988 to 1993 year-classes were weak (Fig. 7;

---

[2] Approximately because the difference depends on the rates of natural mortality and the steepness of the stock-recruitment relationship.

Table 2. Numbers-at-age (females) corresponding to the mode of the posterior for the base-case analysis (millions)

Year	Age														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+
1979	27.22	13.41	8.23	5.43	2.84	3.79	5.21	5.56	4.51	1.85	1.47	1.17	0.96	0.79	3.62
1980	18.65	22.26	10.95	6.71	4.43	2.31	3.09	4.24	4.53	3.67	1.51	1.20	0.96	0.78	3.60
1981	7.41	15.24	18.16	8.92	5.46	3.60	1.88	2.51	3.45	3.68	2.98	1.22	0.97	0.78	3.56
1982	7.72	6.06	12.45	14.83	7.28	4.46	2.94	1.53	2.04	2.81	3.00	2.43	1.00	0.79	3.54
1983	9.99	6.31	4.95	10.15	12.08	5.93	3.62	2.39	1.24	1.66	2.29	2.44	1.98	0.81	3.53
1984	10.46	8.16	5.15	4.03	8.26	9.82	4.81	2.94	1.94	1.01	1.35	1.86	1.99	1.61	3.53
1985	19.93	8.54	6.65	4.19	3.27	6.68	7.93	3.89	2.38	1.57	0.82	1.09	1.51	1.61	4.17
1986	25.84	16.28	6.96	5.41	3.40	2.65	5.40	6.42	3.15	1.92	1.27	0.66	0.89	1.22	4.69
1987	29.05	21.03	13.18	5.62	4.36	2.73	2.13	4.34	5.17	2.54	1.55	1.03	0.54	0.72	4.81
1988	20.16	23.55	16.98	10.64	4.51	3.48	2.18	1.70	3.48	4.15	2.04	1.25	0.83	0.43	4.46
1989	7.66	16.40	19.05	13.69	8.57	3.62	2.80	1.76	1.37	2.82	3.35	1.65	1.01	0.67	3.98
1990	2.36	6.22	13.26	15.37	11.04	6.90	2.92	2.26	1.42	1.11	2.29	2.72	1.34	0.83	3.79
1991	4.09	1.92	5.03	10.69	12.37	8.86	5.53	2.34	1.82	1.14	0.89	1.85	2.20	1.08	3.74
1992	5.18	3.31	1.55	4.02	8.50	9.79	6.99	4.37	1.86	1.45	0.91	0.72	1.48	1.76	3.88
1993	3.88	4.21	2.68	1.24	3.21	6.78	7.81	5.57	3.48	1.48	1.15	0.73	0.57	1.19	4.55
1994	4.05	3.15	3.41	2.15	0.99	2.56	5.37	6.18	4.40	2.75	1.17	0.91	0.58	0.46	4.59
1995	78.31	3.29	2.55	2.74	1.72	0.79	2.03	4.25	4.90	3.50	2.19	0.93	0.73	0.46	4.04
1996	42.57	63.87	2.65	2.04	2.19	1.37	0.63	1.62	3.40	3.92	2.81	1.76	0.75	0.59	3.63
1997	2.68	34.55	51.55	2.12	1.63	1.73	1.09	0.50	1.29	2.70	3.11	2.23	1.40	0.60	3.37
1998	13.00	2.17	27.87	41.37	1.66	1.26	1.34	0.84	0.39	1.00	2.09	2.41	1.73	1.09	3.08
1999	1.92	10.49	1.72	22.10	32.74	1.31	0.96	1.03	0.65	0.30	0.77	1.62	1.86	1.34	3.23

Table 2). The reduction in spawner biomass from 1991 to 1993 is a consequence of the fish from the 1988 and 1989 year-classes being smaller than expected (Punt and Smith 2001).

Figure 8 *left* shows the time-trajectory of spawner biomass and year-class strength for assessments with different final years. The estimates of (female) spawner biomass are relatively consistent from one year to another, excepting only the assessment based on data up to 1994. The sensitivity of the 1994 assessment is readily explained by the fact that it ignores the 1995 egg-production estimate. There is a marked 'retrospective pattern' (Sinclair *et al.* 1991; Mohn 1993) in the recruitment anomalies for the 1994 and 1995 year-classes. This is a consequence of the prior that is placed on the recruitment residuals (Eqn A.11). The recruitment residuals will be assumed to be 0 (i.e. year-class strength equals the value expected from the stock-recruitment relationship) until data indicate otherwise. Figure 8 *left* confirms the value of the data from the discards. The 1994 and 1995 year-classes had only begun to enter the fishery in 1996 but were already relatively well determined by the data used in the assessment.

Sensitivity tests

Table 3 lists the results of a series of sensitivity tests. These are summarized by nine quantities:

(a) B_0, the virgin (female) spawner biomass (defined in terms of average mass-at-age, and values of zero for the recruitment residuals and fishing mortality-at-age);

(b) the (female) spawner biomass in 1979 and 1999;

(c) the ratio of the spawner biomass in 1986, 1993 and 1999 to B_0;

(d) the current (1999) fishing mortality by subfishery; and

(e) the 1994 recruitment anomaly, i.e. the ratio of the number of fish of age 0 during 1994 to the value expected from the (deterministic) stock-recruitment relationship.

The first three quantities examine the sensitivity of the overall level of spawner biomass to the changes considered. The next five quantities examine recent trends in spawner biomass, and the last quantity examines how the size of the 1994 year-class changes.

The estimates of current and virgin biomass and of recent levels of fishing mortality are very sensitive to any assumed bias in the egg production estimates. In contrast, the overall trend, and the fit of the model to the data as reflected by the size of the negative log-likelihood, are relatively insensitive to this bias (Table 3; Fig. 9). The data are unable to determine the level of bias associated with the egg production estimates over a relatively wide range (~95% confidence intervals from 0.34 to 1.89). Unfortunately, the values for most of the quantities of interest to management (except the relative strengths of the various year-classes) are very sensitive to the assumed level of this bias (Fig. 10). The inability to identify the bias is perhaps surprising because most age-structured stock assessments do not include estimates of 'absolute' abundance and yet obtain (apparently) relatively precise estimates of current abundance. However, this may be an artefact of most age-

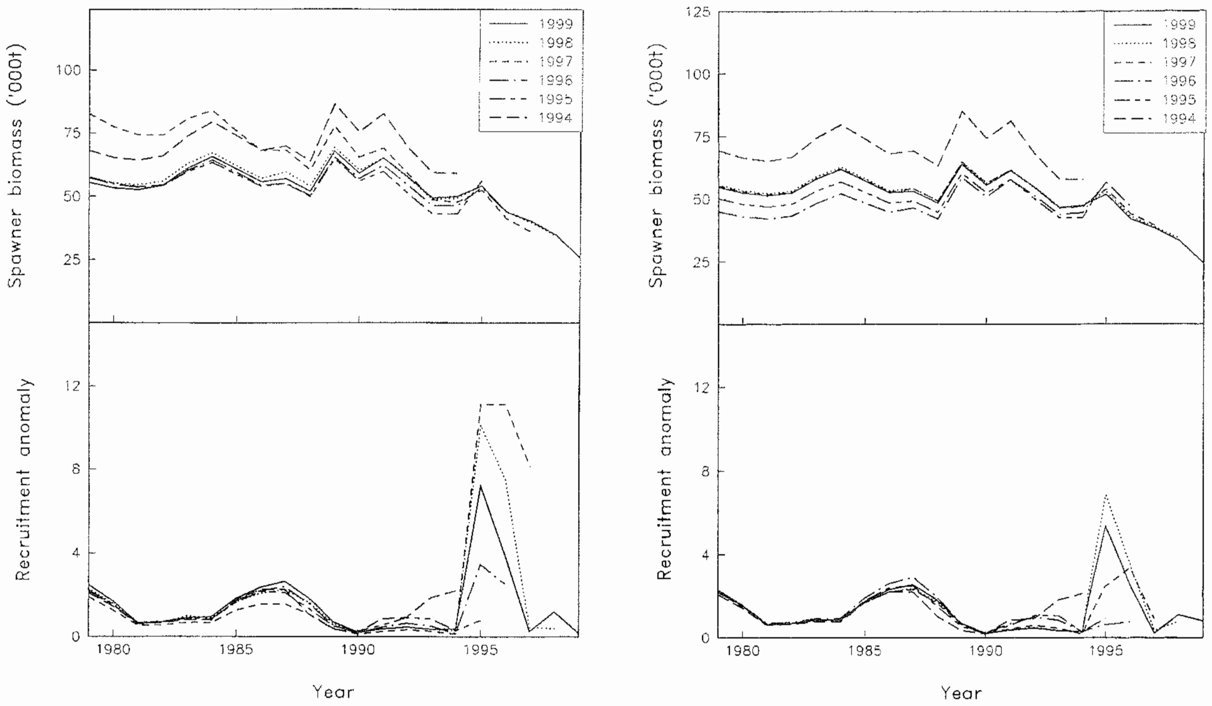


Fig. 8. Time-trajectories of spawner biomass and recruitment anomaly for analyses that vary the final year of the assessment. Results are shown for analyses that *(left)* account for and *(right)* ignore the information on discards.

based assessments being for overfished North Atlantic and North Sea stocks for which there are strong signals in catch rates and the age-composition of the catches. In this case, the inability to distinguish between levels of bias is therefore probably a reflection of the catch rate and age-composition data being relatively uninformative regarding absolute (in contrast to relative) abundance.

The results are insensitive to changing the weights assigned to the different data sources. The current stock size, current depletion and the size of the 1994 year-class are slightly lower if standardized catch rate is assumed to be proportional to the square root of abundance ('CPUE ∝ √biomass' in Table 3). Ignoring the catch rate data altogether ('Ignore catch rate data' in Table 3) and leaving out one but not both catch rate series has little effect on the results. The latter indicates that, once allowance is made for the components of the population on which each subfishery concentrates, the catch rate data for the two subfisheries are, in fact, providing complementary rather than contradictory information. Ignoring the discard data has little effect on the estimate of the 1999 biomass. However, the size of the 1994 year-class is increased substantially compared with the base-case.

Results are also shown in Table 3 for the assumption that length-at-age follows a time- and cohort-invariant von Bertalanffy growth curve (Method 1 of Punt and Smith 2001). The results are very sensitive to the method used to determine mean length- and mass-at-age. Method 1 leads to a lower value for B_0 but to a larger spawner biomass in 1999. The estimate of the 1994 recruitment anomaly for Method 1 is less than half of that for the base-case analysis.

Risk analysis

The results of the risk analysis are summarized by time-trajectories (2000–2019) of female spawner biomass for given levels of TAC, and the probability of dropping below 40% of B_0 after 5, 10 and 20 years for a range of future TACs. Sensitivity is explored to changes in the assumed level of bias associated with the egg production estimates.

The model predicts a marked increase in (female) spawner biomass as the strong 1994 and 1995 year-classes reach maturity, followed by a gradual reduction in biomass as these year-classes die out (Fig. 11). The assumption of a length-at-maturity of 70 cm implies that the strong 1994 year-class is immature in 1999 but fully mature in 2000. Recruitment to the 'spawning' and 'non-spawning' subfisheries is gradual (Fig. 6) so the increase in the biomass available to these subfisheries is not as sudden as is evident in Fig. 11. The 'shape' of the trajectories of spawner biomass in Fig. 11 is similar for the base-case analysis and the sensitivity tests that examine the implications of bias in the egg-production estimates and changing the method used to calculate mean length- and mass-at-age, but there are considerable differences in scale. For example, the virgin (female) spawner biomass is estimated to be 47000 t for the base-case analysis, whereas it is estimated to be only 30000 t

Table 3. Estimates for nine quantities of interest to management

Results are shown for the base-case analysis and the 16 tests of sensitivity. Biomass and fishing mortality units are tonnes and year^{-1}, respectively

Specification	B_0	$\tilde{B}_{79}$	$\tilde{B}_{99}$	$\tilde{B}_{86}/B_0$	$\tilde{B}_{93}/B_0$	$\tilde{B}_{99}/B_0$	F_{99}^1	F_{99}^2	R_{94}
Base-case	46602	55382	25702	1.195	1.057	0.552	0.124	0.038	7.18
No egg estimates	363065	458584	266500	1.262	1.143	0.734	0.012	0.004	7.08
Halve egg estimates	30466	34502	13623	1.151	1.010	0.447	0.239	0.061	7.33
Double egg estimates	86235	107324	55474	1.242	1.104	0.643	0.057	0.020	7.01
CPUE ∝ √biomass	45741	58272	24427	1.246	1.057	0.534	0.129	0.045	6.31
VB growth curve	38505	48447	27099	1.337	1.510	0.704	0.126	0.058	3.35
Use ageing error	46343	67110	26238	1.287	0.973	0.566	0.114	0.034	9.87
$h = 0.85$	46546	55370	25698	1.196	1.058	0.552	0.124	0.038	7.18
$h = 0.95$	46651	55393	25705	1.194	1.056	0.551	0.124	0.038	7.18
$\sigma_q = 0.2$	46621	54610	25971	1.203	1.071	0.557	0.122	0.037	7.39
$\sigma_q = 0.4$	46570	55696	25606	1.193	1.052	0.550	0.125	0.039	7.10
$N = 40$	46757	54775	25598	1.184	1.049	0.547	0.124	0.036	7.55
$N = 60$	46515	55928	25781	1.203	1.063	0.554	0.125	0.040	6.87
Ignore discard-at-age data	47938	56031	25391	1.161	1.020	0.530	0.122	0.034	9.24
Ignore catch rate data	46511	55937	25484	1.188	1.047	0.548	0.126	0.039	6.99
No 'spawning' catch rate data	46715	55004	26227	1.175	1.062	0.561	0.123	0.038	7.14
No 'non-spawning' catch rate data	46747	57815	24933	1.218	1.038	0.533	0.127	0.040	6.89

for the 'halve egg estimate' sensitivity test. The results based on Method 1 for determining length- and mass-at-age are the least optimistic of those in Fig. 11. One of the reasons for the optimistic results for the base-case assessment compared with those for the Method 1 sensitivity test is that the projections all assume that, in the future, length- and mass-at-age equal their expected values. The strong 1995 and (particularly) 1994 year-classes appear to be growing slower than might be expected from the von Bertalanffy growth curve (Punt and Smith 2001). The assumption regarding future mass-at-age therefore leads to an increase in mass-at-age at the start of 2000 for these cohorts beyond that which would be expected simply from the growth alone.

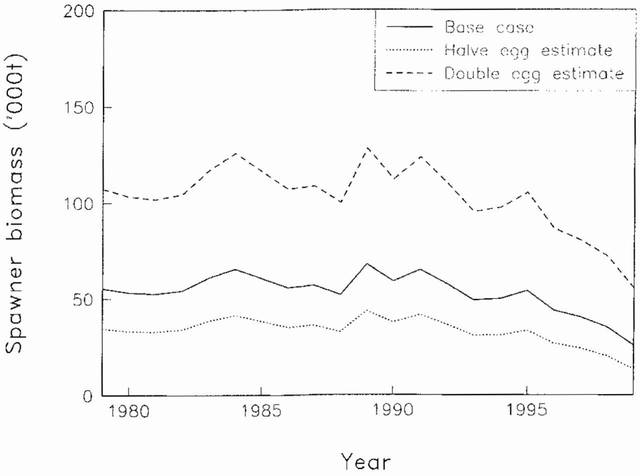


Fig. 9. Time-trajectories of (female) spawner biomass. Results are shown for the base-case analysis and the sensitivity tests in which the assumed level of bias of the egg production estimates is varied.

Figure 12 shows the probability of not dropping below 40% of B_0 for *TAC*s from 1000 to 20000 t per annum over the next 20 years. Results are shown in Fig. 12 for the four analyses considered in Fig. 11. The probability of dropping below 40% B_0 over the next five years is less than 10% for TACs <~10000 t for all situations except that in which length-at-age follows a von Bertalanffy growth curve. In contrast, if a 20-year time horizon is considered, a 10000 t TAC leads to a >50% probability of dropping below 40% B_0 if the 'halve egg estimate' situation is correct (Fig. 12*b*). The results of the projections are, as expected, very sensitive to which situation turns out to be closest to the truth. If TACs are set to achieve a 50% probability of being above 40% B_0 in 2019, the TAC would be 14500 t, 9500 t, >20000 t or 9700 t, depending on which of the four situations is correct. The results based on the 'double egg estimate' assessment are the most optimistic whereas those based on the 'halve egg estimate' and Method 1 assessments are the least optimistic.

The results of the present assessment are generally very optimistic for the next five to ten years. Although this is the best estimate from the assessment, it should be recognized that the ability to estimate risk is often very poor (e.g. Cordue and Francis 1994). The assessed levels of future risk are very dependent on the sizes of the 1994 and 1995 year-classes. There are many instances of apparently strong year-

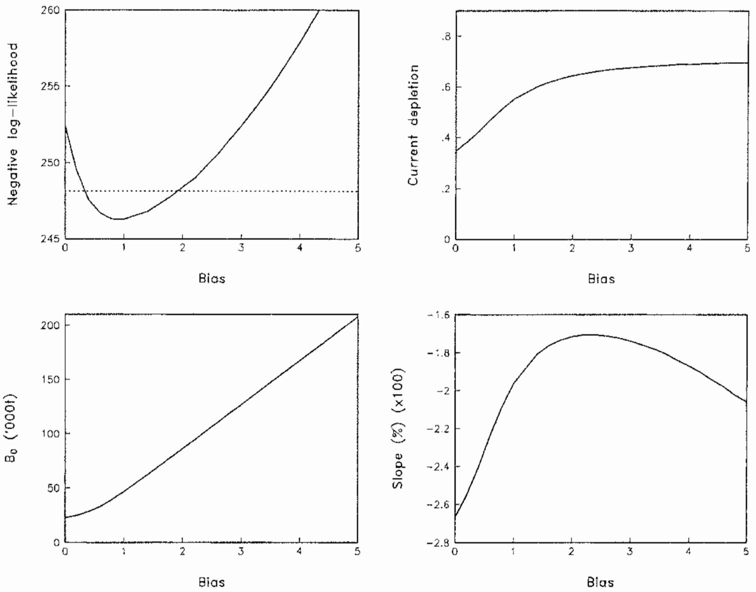


Fig. 10. Value of the negative of the logarithm of the likelihood function (ignoring constants), the current depletion ($\tilde{B}_{99}/B_0$), B_0, and the slope of a regression of the logarithms of spawner biomass from 1986 to 1996 on time (multiplied by 100 for ease of presentation), against the assumed level of bias in the egg production estimates. The dotted line in the upper left panel indicates approximate 95% limits for this bias.

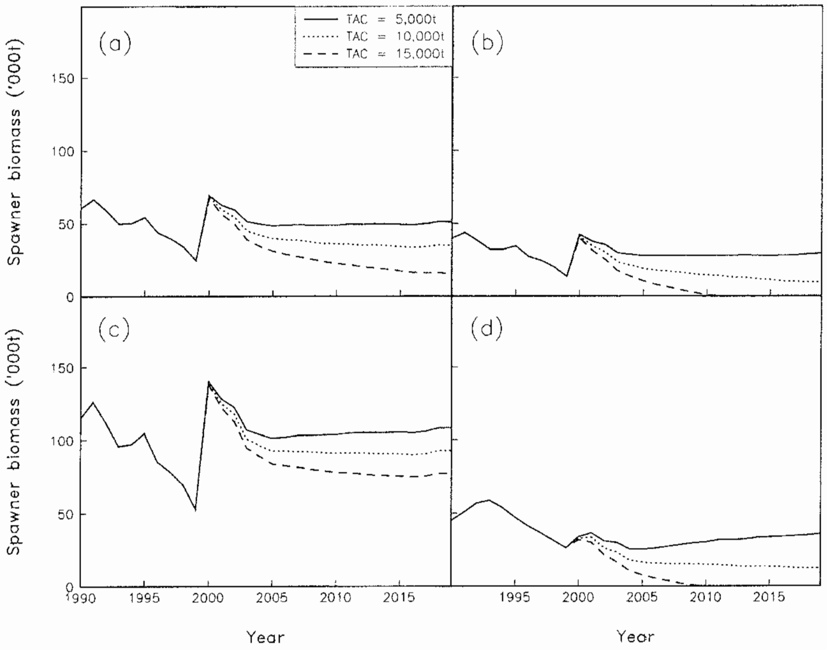


Fig. 11. Posterior median time-trajectories (1990–2019) of spawner biomass for three levels of future TAC. Results are shown for *(a)* the base-case assessment, *(b)* the 'halve egg estimates' sensitivity test, *(c)* the 'double egg estimates' sensitivity test, and *(d)* an assessment based on assuming that length-at-age follows a time- and cohort-invariant von Bertalanffy growth curve (Method 1).

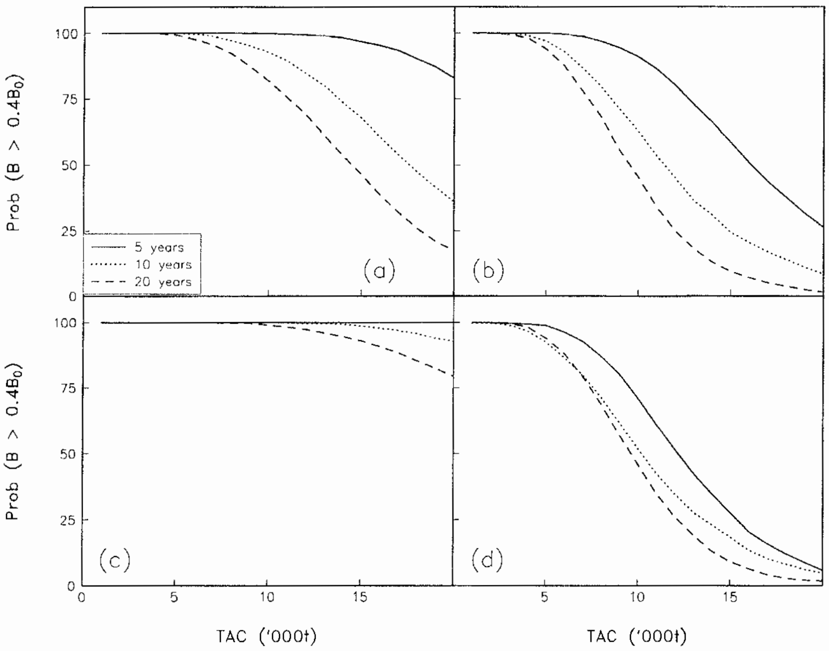


Fig. 12. Probability of not dropping below 40% of B_0 after 5, 10 and 20 years as a function of the level of future TAC. Results are shown for the four assessments considered in Fig. 11.

classes turning out to be much smaller than initially estimated (Fogarty *et al.* 1991; Pearson *et al.* 1999). It is also well known (e.g. Pope 1972) that the strengths of recent year-classes are poorly determined by age-based methods of stock assessment.

The results in Figs 11 and 12 are based on the value for B_0 that arises from assuming that the recruitment residual for each age-class is zero (deterministic B_0). However, given the log-normal error model assumed for recruitment variability, the expected unfished biomass is larger than the deterministic B_0 by roughly $e^{\sigma_r^2/2}$ if steepness is 1 (1.65 for the choice $\sigma_r = 1$). The results of 1000 simulations for 10000 years in the absence of fishing resulted in 95% of the projections lying between 93% and 293% of the deterministic B_0. If the results in Figs 11 and 12 had been expressed relative to the average unfished level, they would have been markedly less optimistic. How to define B_0 (deterministic or average unfished) for expressing the results of a risk analysis is, however, unclear. The average unfished biomass is clearly the correct choice if reference is being made to the size of the biomass relative to its size in an unfished state. However, the deterministic B_0 is probably more appropriate if the concern is reduction in recruitment at low levels of spawner biomass.

Management implications

This paper presents the first 'formal' assessment of blue grenadier in Australia. Prior to 1997, assessments were based primarily on inferences from swept area trawl surveys (Chesson and Staples 1995), egg production estimates of abundance (Bulman *et al.* 1999), and examinations of catch rate and age/size-composition data. However, unlike the present assessment, no attempt was made to 'synthesize' all of the available information into a single picture of the historical and current status of the resource. Although the fits to some of the data sources are relatively imprecise, the model is nevertheless able to reconcile the differing trends in catch rate for the two subfisheries. In particular, because the 'non-spawning' subfishery concentrates principally on 4–5 age-classes of juveniles and sub-adults, the biomass available to it is subject to considerable variation due to differing year-class strengths. The 'spawning' subfishery, which targets more than 10 age-classes and concentrates on adult fish, is less subject to this variation. Given the marked trends in year-class strength, declines would have occurred in the biomass available to the 'non-spawning' subfishery from 1989 to 1998 even in the absence of a fishery (Fig. 13), although these would not have been quite as marked as those evident from the base-case analysis.

The total mass of fish discarded from 1996 to 1998 by the 'non-spawning' subfishery is estimated to be close to 8000 t, which is similar to the total landings by that fishery during these years. The observed amount of fish discarded in 1999 is much lower than that in 1998 and should reduce further as the 1994 and 1995 year-classes reach marketable size. Nevertheless, the discarding of 8000 t amounts to a substantial loss in potential yield, the effect of which could be even greater than currently perceived if the egg production estimates are positively biased.

General remarks

The importance of the discard data to the blue grenadier assessment cannot be over-emphasized, because only through use of these data can quantitative estimates of year-class strength be obtained prior to the year-class recruiting to the 'non-spawning' subfishery. This is evident from Fig. 8*right*, which shows that, without the information about the discards, the relative strength of the 1994 cohort would not have been detected before 1997. In contrast, this is detected in 1996 when the discard data are included in the assessment. Few assessments explicitly include data for discards as part of the information included in the likelihood function. The results of this paper indicate the value of doing this as it becomes possible to identify strong year-classes before they enter the fishery.

The level of variation in year-class strength (historically but particularly recently) confirms the highly fluctuating nature of the blue grenadier resource. Previous model-based risk analyses for blue grenadier have been based on the assumption of no variation about the stock-recruitment relationship (N. Klaer, CMR, personal communication). Such analyses would clearly underestimate the uncertainty surrounding population projections. The realization that fluctuations in blue grenadier year-class strength might be greater than previously thought is consistent with the fact that recent assessments of eastern gemfish *Rexea solandri* and blue warehou, *Seriolella brama*, indicated greater than previously believed levels of variability in year-class strength. Variability of blue grenadier year-class strength in New Zealand has also been shown to be high (Ballara *et al.* 1998).

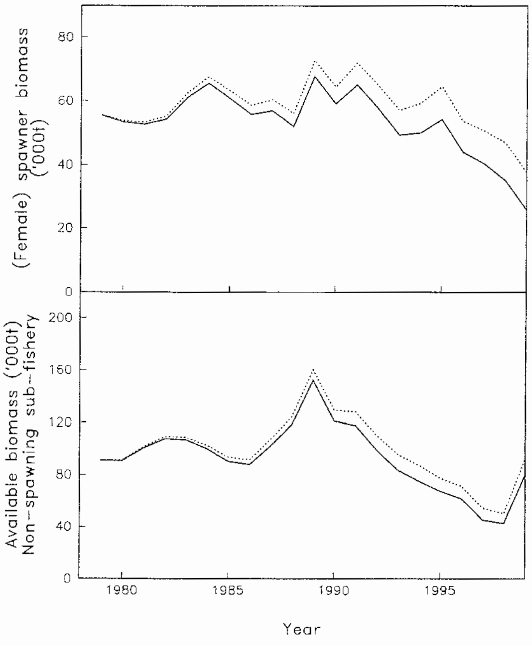


Fig. 13. Time-trajectories of (female) spawner biomass and the biomass (both sexes combined) available to the 'non-spawning' subfishery for the base-case analysis. The dotted lines correspond to projecting from 1979 to 1999 under the assumption of zero fishing mortality.

Acknowledgments

We thank the remaining members of the BGAG for their comments on the analyses presented in this paper. Support for this work was received from the BGAG budget (AEP, DCS, and MH) and FRDC grant 97/115 'Development of priority stock assessments for the South East Fishery' (RBT). Sandy Morison and Ian Knuckey (Marine and Freshwater Resources Institute) provided the recent length–frequency data, Corey Green and Simon Robertson (Central Ageing Facility) did the ageing, and AFMA supplied the catch and effort data.

References

Ballara, S. L., Cordue, P. L., and Livingston, M. E. (1997). A review of the 1994–95 hoki fishery and assessment of hoki stocks for 1996. *New Zealand Fishery Assessment Research Document* 97/10. 44 pp.

Ballara, S. L., Livingston, M. E., and Cordue, P. L. (1998). A review of the 1995–96 hoki fishery and assessment of hoki stocks for 1997. New Zealand Fishery Assessment Research Document No. 98/1. 56 pp.

Bulman, C. M., Koslow, J. A., and Haskard, K. A. (1999). Estimation of the spawning stock biomass of blue grenadier (*Macruronus novaezelandie*) off western Tasmania based upon the annual egg production method. *Marine and Freshwater Research* **50**, 197–207.

Burnham, K. P., and Anderson, D. R. (1998). 'Model Selection and Inference. A Practical Information-Theoretic Approach.' (Springer: New York.)

Butterworth, D. S., and Punt, A. E. (1992). Assessments of the East-Greenland–Iceland fin whale stock. *Reports of the International Whaling Commission* **42**, 671–96.

Butterworth, D. S., Cochrane, K. L., and De Oliveira, J. A. A. (1997). Management procedures: a better way to manage fisheries? The South African experience. In 'Global Trends: Fisheries Management'. (Eds E. K. Pikitch, D. D. Huppert and M. P. Sissenwine). pp. 83–90. (American Fisheries Society Symposium 20, Bethesda, MD.)

Chesson, J., and Staples, D. J. (1995). Blue Grenadier 1994, Stock Assessment Report, Blue Grenadier Assessment Group, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Cooke, J. G., and Beddington, J. R. (1984). The relationship between catch rates and abundance in fisheries. *IMA Journal of Mathematics Applied in Medicine and Biology* **1**, 391–405.

Cordue, P. L., and Francis, R. I. C. C. (1994). Accuracy and choice in risk estimation for fisheries assessment. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 817–29.

Fogarty, M. J., Sissenwine, M. P, and Cohen, E. B. (1991). Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution* **6**, 241–6.

Fournier, D., and Archibald, C. P. (1982). A general theory for analyzing catch at age data. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1195–207.

Francis, R. I. C. C. (1992). Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 922–30.

Gelman, A., Carlin, J. B., Stern, H. S., and Rubin, D. B. (1995). 'Bayesian Data Analysis.' (Chapman and Hall: London.)

Gunn, J. S., Bruce, B. D., Furlani, D. M., Thresher, R. E., and Blaber, S. J. M. (1989). Timing and location of spawning of blue grenadier, *Macruronus novaezelandie* (Teleostei : Merlucciidae) in Australian coastal waters. *Australian Journal of Marine and Freshwater Research* **40**, 97–112.

Hastings, W. K. (1970). Monte Carlo sampling methods using Markov chains and their applications. *Biometrika* **57**, 97–109.

Kalish, J. M., Johnston, J. M., Smith, D. C., Morison, A. K., and Robertson, S. G. (1997). Use of the bomb radiocarbon chronometer for age validation in the blue grenadier *Macruronus novaezelandiae*. *Marine Biology* **128**, 557–63.

Klaer, N. L. (1994). Methods for standardization of catch/effort and data requirements. In 'Population Dynamics for Fisheries Management'. (Ed. D. A. Hancock.) pp. 86–90. (Australian Government Publishing Service: Canberra.)

Knuckey, I. A., Grieve, C., and Smith, D. C. (1999). Evolution of the integrated scientific monitoring programme in Australia's South East Fishery. In 'Proceedings of the International Conference on Integrated Fisheries Monitoring. Sydney, Australia, 1–5 February 1999'. (Ed. C. P. Nolan.) pp. 231–48. (FAO: Rome.)

Livingston, M. E., Vignaux, M., and Schofield, K. A. (1997). Estimating the annual proportion of nonspawning adults in New Zealand hoki, *Macruronus novaezelandiae*. *Fishery Bulletin* (*US*) **95**, 99–113.

McAllister, M. K., and Ianelli, J. N. (1997). Bayesian stock assessment using catch-age data and the sampling-importance resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 284–300.

McAllister, M. K., Pikitch, E. K., Punt, A. E., and Hilborn, R. (1994). A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 2673–87.

Methot, R. (1989). Synthetic estimates of historical abundance and mortality for northern anchovy. *American Fisheries Society Symposium* **6**, 66–82.

Methot, R. (1990). Synthesis model: an adaptable framework for analysis of diverse stock assessment data. *Bulletin of the International North Pacific Fisheries Commission* **50**, 259–77.

Milton, D. A., and Shaklee, J. B. (1987). Biochemical genetics and population structure of blue grenadier, *Macruronus novaezelandie* (Hector) (Pisces : Meluicciidae), from Australian waters. *Australian Journal of Marine and Freshwater Research* **38**, 727–42.

Mohn, R. K. (1993). Bootstrap estimates of ADAPT parameters, their projection in risk analysis and their retrospective patterns. In 'Risk Evaluation and Biological Reference Points for Fisheries Management.' (Eds S. J. Smith, J. J. Hunt and D. Rivard.) pp. 173–84. *Canadian Journal of Fisheries and Aquatic Sciences* (*Special Publication*) 120.

Morison, A. K., Robertson, S. G., and Smith, D. C. (1998). An integrated system for production fish ageing: image analysis and quality assurance. *North American Journal of Fisheries Management* **18**, 587–98.

Otter Research Ltd. (1994). 'An Introduction to AD Model Builder.' (Otter Research Ltd: Nanaimo, Canada.)

Pearson, W. H., Elston, R. A., Beinert, R. W., Drum, A. S., and Antrim, L. D. (1999). Why did the Prince William Sound, Alaska, Pacific herring (*Clupea pallasi*) fisheries collapse in 1993 and 1994? Review of hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 711–37.

Pope, J. G. (1972). An investigation of the accuracy of virtual population analysis using cohort analysis. *Research Bulletin of International Commission for Northwest Atlantic Fisheries* **9**, 65–74.

Punt, A. E., and Hilborn, R. (1997). Fisheries stock assessment and decision analysis: a review of the Bayesian approach. *Reviews in Fish Biology and Fisheries* **7**, 35–63.

Punt, A. E., and Smith, D. C (2001). Assessments of species in the Australian South East Fishery can be sensitive to the method used to convert from size- to age-composition data. *Marine and Freshwater Research* **52**, 683–90.

Punt, A. E., Smith, A. D. M., and Cui, G. (2001). Review of progress in the introduction of management strategy evaluation (MSE) approaches in Australia's South East Fishery. *Marine and Freshwater Research* **52**, 719–26.

Richards, L. J. (1991). Use of contradictory data sources in stock assessments. *Fisheries Research* **11**, 225–38.

Sinclair, A., Gascon, D., O'Boyle, R., Rivard, D., and Gavaris, S. (1991). Consistency of some Northwest Atlantic groundfish stock assessments. *NAFO Scientific Council* **16**, 59–77.

Smith, A. D. M. (1994). Blue grenadier, *Macruronus novaezelandiae*. *In* 'The South East Fishery.' (Ed. R. D. J. Tilzey.) pp. 137–48. (Bureau of Resource Sciences: Canberra.)

Smith, A. D. M., Sainsbury, K. J., and Stevens, R. A. (1999). Implementing effective fisheries management systems – management strategy evaluation and the Australian partnership approach. *ICES Journal of Marine Science* **56**, 967–79.

Smith, D. C. (1998*a*). Blue Grenadier 1998, Stock Assessment Report, Blue Grenadier Assessment Group, South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Smith, D. C. (1998*b*). Re-ageing of 1980's Blue Grenadier Otolith Collections, Analysis of Catch and Effort Data and Subsequent Stock Assessment Workshop. Final Report to Australian Fisheries Management Authority. ARF Project 96/97–6. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Smith, D. C., Smith, A. D. M., and Punt, A. E. (2001). Approach and process for stock assessment in the South East Fishery, Australia: a perspective. *Marine and Freshwater Research* **52**, 671–81.

Smith, D. C, Huber, D., Woolcock, J., Withell, A., and Williams, S. (1995). Western Bass Strait Trawl Fishery Assessment Program. Final Report to FRDC, FRDC Project 86/39. (Marine and Freshwater Resources Institute: Queenscliff, Australia.)

Thresher, R. E., Bruce, D. B., Furlani, D. M., and Gunn, J. S. (1989). Distribution, advection and growth of larvae of the southern temperate gadoid *Macruronus novaezelandiae* (Teleostei : Merlucciidae), in Australian coastal waters. *Fishery Bulletin* (*US*) **87**, 17–28.

Vignaux, M. (1993) Catch per unit of effort (CPUE) analysis of the hoki fishery 1987–92. *New Zealand Fishery Assessment Research Document* 93/14. 23 pp.

Manuscript received 23 September 1999; revised and accepted 2 June 2000

Appendix A. Population dynamics model and likelihood function

Basic dynamics

The dynamics of animals of sex s aged 1 and above are governed by the equation

$$N^s_{y+1,a} = \begin{cases} N^s_{y+1,1} & \text{if } a = 1 \\ N^s_{y,a-1}\, e^{-Z^s_{y,a-1}} & \text{if } 1 < a < x \\ N^s_{y,x} e^{-Z^s_{y,x}} + N^s_{y,x-1} e^{-Z^s_{y,x-1}} & \text{if } a = x \end{cases} \quad \text{(A.1)}$$

where $N^s_{y,a}$ is the number of fish of sex s and age a at the start of year y (where y runs from 1 to t),

$Z^s_{y,a}$ is the total mortality on fish of sex s and age a during year y:

$$Z^s_{y,a} = M^s + S^1_{y,a} F^1_y + S^2_{y,a} F^2_y \quad \text{(A.2)}$$

M^s is the (age-independent) rate of natural mortality for animals of sex s,

$S^f_{y,a}$ is the vulnerability by subfishery f (f=1 for the 'spawning' subfishery, and f=2 for the 'non-spawning' subfishery) on fish of age a during year y,

F^f_y is the fully-selected fishing mortality by subfishery f during year y, and

x is the maximum age-class (taken to be a plus-group).

The number of 1-year-olds of sex s at the start of year y+1 is related to the spawner biomass of females in the middle of the preceding year according to the equation:

$$N^s_{y+1,1} = [0.5\ \tilde{B}_y/(\alpha + \beta\, \tilde{B}_y)]e^{\varepsilon_y} \quad \text{(A.3)}$$

where $\tilde{B}_y$ is the spawner biomass of females in the middle of year y:

$$\tilde{B}_y = \mu \sum_{a=1}^{x} f_{y,a}\, w_{y,a}\, N^f_{y,a}\, e^{-Z^f_{y,a}/2} \quad \text{(A.4)}$$

μ is the proportion of mature females that spawn each year,

$f_{y,a}$ is the proportion of females of age a that are mature during year y:

$$f_{y,a} = \begin{cases} 1 & \text{if } L_{y,a} \geq 70 \text{ cm} \\ 0 & \text{otherwise} \end{cases}$$

$w_{y,a}$ is the mass of a fish of age a in the middle of the year y,

$L_{y,a}$ is the mean length of a fish of age a during year y (given either by the empirical mean length-at-age each year, or from the fit of a von Bertalanffy growth curve),

α, β are the parameters of the stock-recruitment relationship, and

ε_y is the recruitment residual for year y (for ease of presentation, $\exp(\varepsilon_y)$ will be referred to as the recruitment anomaly for year y).

The values for α and β are determined from the steepness of the stock-recruitment relationship (h) and the virgin biomass (B_0) using the equations of Francis (1992). The assumption that maturity is knife-edged at 70 cm is very crude and a research project has been proposed to provide a more realistic picture of maturity as a function of length. In principle, the probability of being mature-at-length could have been assumed to be the same as vulnerability to the 'spawning' subfishery. This assumption has been made for assessments of blue grenadier in New Zealand (e.g. McAllister *et al.* 1994). However, it may be substantially in error for blue grenadier in Australia because it is known that fish of different sizes arrive on the spawning grounds at different times, and that some immature fish are caught during the 'spawning' subfishery.

The specifications for the numbers-at-age at the start of 1979 are based on the assumption that the stock would have been close to its unexploited equilibrium size at that time:

$$N^s_{1979,a} = 0.5 \begin{cases} R_0 e^{-(a-1)M^s} e^{\varepsilon_a} & \text{if } a<x \\ R_0 e^{-(x-1)M^s}/(1-e^{-M^s}) & \text{if } a=x \end{cases} \quad \text{(A.5)}$$

where R_0 is the expected number of 1-year-olds at unexploited equilibrium (the sex ratio at age 1 is taken to be 1:1), and

ε_a is the recruitment residual for age a.

The equation for the plus-group does not include a contribution by a recruitment residual because this group comprises several age-classes, which will largely damp out the impact of inter-annual variation in year-class strength.

Vulnerability

The vulnerability of the gear is governed by a logistic curve that permits the probability of capture to drop off with length:

$$S^f_{y,a} = \begin{cases} (1 + e^{-\ell n 19(L_{y,a}-L^f_{50})/(L^f_{95}-L^f_{50})})^{-1} & \text{if } L_{y,a} \leq L^f_{95} \\ (1 + e^{-\ell n 19(L_{y,a}-L^f_{50})/(L^f_{95}-L^f_{50})})^{-1} e^{-\lambda^f (L_{y,a}-L^f_{95})} & \text{otherwise} \end{cases} \quad \text{(A.6)}$$

where L^f_{50} is the length-at-50%-vulnerability for subfishery f,

L^f_{95} is the length-at-95%-vulnerability for subfishery f, and

λ^f is the "vulnerability slope" for subfishery f.

The vulnerability pattern for the 'spawning' subfishery is assumed to be asymptotic (i.e. λ = 0for the 'spawning' subfishery).

Catches

The catch (in number) of fish of age a by subfishery f during year y, $\hat{C}^f_y$, and the number of fish of age a discarded by subfishery f, during year y, $\hat{D}^f_y$, are given by the equations:

$$\hat{C}^f_{y,a} = \sum_s \frac{(1-P_{y,a}) S^f_{y,a} F^f_y}{Z^s_{y,a}} N^s_{y,a}(1-e^{-Z^s_{y,a}}) \quad \text{(A.7}a\text{)}$$

$$\tilde{D}^f_{y,a} = \sum_s \frac{P_{y,a} S^f_{y,a} F^f_y}{Z^s_{y,a}} N^s_{y,a}(1-e^{-Z^s_{y,a}}) \quad \text{(A.7}b\text{)}$$

where $P_{y,a}$ is the probability of discarding a fish of age a during year y:

$$P_{y,a} = \frac{\gamma(\sum_s N^s_{y,1})^{\phi} / \max_{y'}(\sum_{s'} N^{s'}_{y',1})^{\phi}}{1 + e^{-(L_a - L^D_{50})/\delta}} \quad \text{(A.8)}$$

γ is the maximum possible discard rate for the largest year-class,

L^D_{50} is the length at which discarding is half the maximum possible rate,

δ is the parameter that determines the width of the relationship between length and the discard probability, and

ϕ is the parameter that controls the extent of density-dependent discarding.

The rate of discarding is therefore assumed to be related only to the size of the year-class at birth; the impact of density-dependence on the rate of discarding is assumed to be constant during the whole of an animal's life. The first assumption will be violated to some extent because *inter alia* the rate of discarding will depend on the abundance of other year-classes in the population (through high-grading). Violation of the second assumption is probably inconsequential because for older ages the form of the denominator of Eqn (A.8) will mean that $P_{y,a} \approx 0$.

The model estimates of the catch (in mass) by subfishery *f* during year *y*, $\hat{C}^f_y$, and of the mass of fish discarded by subfishery *f* during year *y*, $\hat{D}^f_y$ are given by the equations:

$$\hat{C}^f_y = \sum_{a=1}^{x} w_{y,a} \hat{C}^f_{y,a} \tag{A.9a}$$

$$\hat{D}^f_y = \sum_{a=1}^{x} w_{y,a} \hat{D}^f_{y,a} \tag{A.9b}$$

Eqns (A.9*a*) and (A.9*b*) imply that the (expected) mass of a fish of age *a* that is discarded is the same as the (expected) mass of a fish of age *a* that is retained.

Likelihood function

The negative of the logarithm of the likelihood function includes five contributions. These relate to minimizing the sizes of the recruitment residuals, fitting the observed catches / discards by fleet, fitting the observed catch / discard age-compositions, fitting the catch rate information, and fitting the estimates of spawner biomass from the egg-production method.

$$L = \sum_{i=1}^{5} L_i \tag{A.10}$$

The contribution of the recruitment residuals to the negative of the logarithm of the likelihood function is based on the assumption that the inter-annual fluctuations in year-class strength are independent and log-normally distributed with a CV of σ_r[1]:

$$L_1 = \frac{1}{2\sigma_r^2}\left(\sum_{a=1}^{x-1} \varepsilon_a^2 + \sum_{y=1}^{t-1} \varepsilon_y^2\right) \tag{A.11}$$

The contribution of the observed catch (in mass) information to the negative of the logarithm of the likelihood function is based on the assumption that the errors in measuring the catch in mass are log-normally distributed with a CV of σ_c:

$$L_2 = \frac{1}{2\sigma_c^2} \sum_f \sum_{y=1}^{t} (\ell n C_y^{f,\text{obs}} - \ell n \hat{C}^f_y)^2 \tag{A.12}$$

where $C_y^{f,\text{obs}}$ is the observed catch (in mass) by subfishery *f* during year *y*.

The contribution of the observed mass of discards to the negative of the logarithm of the likelihood function follows Eqn (A.12) except that is replaced by $\hat{D}^f_y$, $\hat{C}^{f,\text{obs}}_y$ is replaced by the observed mass of discards by subfishery *f* during year *y*, and the summations over year are restricted to those years for which estimates of discards are available (1996–99 for the 'non-spawning' subfishery).

The contribution of the age composition information to the negative of the logarithm of the likelihood function is based on the assumption that the age-structure information is determined from a random sample of *N* animals from the catch:

$$L_3 = -\sum_f \sum_y \sum_{a=1}^{15+} N \rho_{y,a}^{f,\text{obs}} \ell n(\hat{\rho}^f_{y,a}) \tag{A.13}$$

where $\rho_{y,a}^{f,\text{obs}}$ is the observed proportion which fish of age *a* made up of the catch during year *y* by subfishery *f*,

$\hat{\rho}^f_{y,a}$ is the model-estimate of the proportion which fish of age *a* made up of the catch during year *y* by subfishery *f*:

$$\hat{\rho}^f_{y,a} = \sum_{a''} \chi_{a,a''} \hat{C}_{y,a''} / \sum_{a'=1}^{x} \hat{C}^f_{y,a'} \tag{A.14}$$

$\chi_{a,a'}$ is the probability that an animal of age a' will be found to be age *a* (the age-reading error matrix – Table A.1 if allowance is made for age-reading error and a diagonal matrix if age-reading error is ignored).

Note that all animals aged 15 and older are treated as a single "age-class" when fitting to the catch proportion-at-age information. This prevents data for older fish (for which there are relatively little data) having a disproportionate influence on the results. The summations over year include only those years for which age-composition data are available. The contribution of the age-composition of the discards follows Eqns (A.13) and (A.14), except that $\hat{\rho}^f_{y,a}$ is replaced by the model-estimate of the proportion which fish of age *a* made up of the discards during year *y* by subfishery *f*, and $\rho_{y,a}^{f,\text{obs}}$ is replaced by the observed proportion which fish of age *a* made up of the discards during year *y* by subfishery *f*.

The contribution of the catch rate data to the negative of the logarithm of the likelihood function is based on the assumption that fluctuations in catchability are log-normally distributed with a CV of σ_q:

$$L_4 = \frac{1}{2\sigma_q^2} \sum_f \sum_y (\ell n\, I^f_y - \ell n\, (q^f B^f_y))^2 \tag{A.15}$$

where q^f is the catchability coefficient for subfishery *f*,

I^f_y is the catch-rate index for subfishery *f* and year *y*, and

B^f_y is the mid-season (available) biomass for subfishery *f* and year *y*:

$$B^f_y = \sum_s \sum_a w_{y,a}(1 - P_{y,a}) S^f_a N^s_{y,a} e^{-Z^s_{y,a}/2} \tag{A.16}$$

The summation over year includes only those years for which catch rate data are available (1986–99).

The contribution of the egg-production estimates to the negative of the logarithm of the likelihood function is given by:

$$L_5 = \sum_{y=1994/5} (\tilde{B}_y - B_y^{\text{obs}})^2 / (2\sigma_y)^2 \tag{A.17}$$

where B_y^{obs} is the estimate of female spawner biomass for year *y* based on the egg-production method, and

σ_y is the standard error of B_y^{obs}.

---

[1] The summation in Eqn (A.11) runs to *x*–1 and *t*–1 because the plus-group (age *x*) is not affected by variability in year-class strength, and because the model is not used to predict the number of 1-year-olds for year *t*+1.

Table A.1. Age-reading error matrix, shown as the percentage of otoliths that were found to be a certain age by a reader (columns) that were assigned to an age (rows) by a second reader

Source: Central Ageing Facility, MAFRI, Queenscliff

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	38	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	62	77	16	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	17	79	65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	1	6	30	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	50	20	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	50	23	7	4	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	20	25	54	50	20	9	3	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	25	15	33	48	26	0	5	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	8	3	22	43	22	16	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	7	4	15	41	21	13	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	2	4	27	53	63	33	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	4	8	5	13	33	25	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	25	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	50	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	50	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0	100

Mar. Freshwater Res., 2001, **52**, 719–26

Review of progress in the introduction of management strategy evaluation (MSE) approaches in Australia's South East Fishery

André E. Punt[A], *Anthony D. M. Smith and Gurong Cui*

CSIRO Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia
[A]Contact address: School of Aquatic and Fisheries Sciences, Box 355020, University of Washington, Seattle, WA 98195-5020, USA

Abstract. The MSE approach provides a simulation-based framework within which harvest strategies, stock assessment methods, performance indicators and research programmes can be compared. This approach has been used in the Australian South East Fishery (SEF) to assess harvest strategies for the over-exploited eastern gemfish resource and to compare different levels of discard monitoring for blue grenadier. The main challenges to use of the MSE approach in the SEF are poorly specified management objectives and the lack of quantitative stock assessments on which to build operating models for many of the species.

Introduction

Australia's South East Fishery (SEF) is a multi-species, multi-sector fishery, the trawl sector of which operates from Barrenjoey Point off New South Wales to Cape Jervis off South Australia (Tilzey 1999). It is managed primarily by means of Total Allowable Catches (TACs), which are set for the 16 key species in the fishery (Table 1). These 16 species constitute approximately 80% of the landed catch (Tilzey 1999). Management actions for all the species in this fishery must be selected to satisfy (to the extent possible) the five legislative objectives of the Australian Fisheries Management Authority (AFMA). These objectives are: conducting management consistent with the principles of ecologically sustainable development (ESD), maximizing economic efficiency, implementing efficient and cost effective management, ensuring accountability to the fishing industry and the Australian community, and achieving government targets in relation to cost recovery.

The TACs for the SEF quota species are set by the AFMA Board (which currently consists of a Chairman, the Managing Director of AFMA, two scientists, a government director, a management consultant and two industry representatives), which, for the SEF, is advised by two Management Advisory Committees (MACs), representing the trawl and non-trawl sectors of the fishery. The scientific advice on which TACs are based is developed by the South East Fishery Assessment Group (SEFAG), which has established several species-specific subgroups[1].

The process of providing scientific advice related to TAC setting for several species therefore originates at the species-specific subgroup level and passes through a variety of other committees (which act to some extent as an internal review process). However, development of this advice has proved (and continues to prove) difficult because AFMA's legislative objectives are not sufficiently explicit at the level of species management. This problem has been overcome for some species by defining more specific objectives. However, some of these specific objectives are in conflict. For example, the specific management objectives for blue grenadier, *Macruronus novaezelandiae*, used to include 'sustainable development of the winter spawning run fishery of blue grenadier off the west coast of Tasmania' and 'maintain the catch per unit effort (CPUE) in the non-spawning fishery above its lowest annual average level from 1986 to 1994' (Tilzey 1999). These objectives are clearly in conflict because achievement of the first objective implies a higher probability of failing to achieve the second objective.

Until recently, the only rule used to assess stock status in the SEF has been the so-called 'CPUE strategy'. This involves assessing whether the catch rate for the last year for which data are available is less or greater than the lowest catch rate over a pre-specified period (usually 1986–94). This 'strategy' has been criticised by both industry and scientists as being inadequate given *inter alia* concerns regarding the relationship between catch rate and abundance (Tilzey 1999). In addition, the 'strategy' is not explicit about what actions will be taken if the catch rate does fall below the threshold.

---

[1] Species-specific subgroups exist for eastern gemfish, orange roughy, blue grenadier, blue warehou and redfish.

10.1071/MF99187 1323-1650/01/040719

Table 1. Status of quantitative assessments for the SEF quota species
N/A, not applicable

Species	Current stock assessment	Projections	MSE status
Blue-eye travalla	No	N/A	N/A
Blue grenadier	Integrated analysis	Yes	Planned for 2000
Blue warehou	Integrated analysis	Yes	N/A
Eastern school whiting	Integrated analysis/ADAPT	No	N/A
Gemfish, eastern	Integrated analysis	Yes	Underway
Gemfish, western	No	N/A	N/A
Jackass morwong	No[A]	N/A	Generic study
John dory	No	N/A	N/A
Ling	Under development[A]	N/A	Generic study
Mirror dory	No	N/A	N/A
Ocean perch	No	N/A	N/A
Orange roughy	Integrated analysis	Yes	Stalled
Redfish	Under development	N/A	N/A
Red royal prawn	No	N/A	N/A
Spotted warehou	Under development[A]	N/A	Generic study
Tiger flathead	No[A]	N/A	Generic study
Silver trevally	No	N/A	N/A

[A] Models have been developed for these species to examine the generic properties of harvest strategies.

The 'Management Strategy Evaluation' (MSE) approach (e.g. Smith 1994) is increasingly being used by SEFAG to develop scientific advice. This approach provides a set of tools that allow four key scientific questions to be addressed:

- evaluation of the extent to which alternative rules for setting future TACs (referred to as harvest strategies[2]) can satisfy the management objectives and hence identify the trade-offs among the objectives corresponding to different harvest strategies;
- evaluation of which methods of stock assessment are able to provide sufficiently reliable estimates of quantities of interest to management (such as current biomass and MSY);
- evaluation of whether proposed performance indices are able to detect the events that they were designed to identify. These events might include those in which the fishery is close to (but not yet in) an undesirable state;
- evaluation of the (management) benefits of research programmes.

A key feature of the MSE approach is that it can explicitly take account of uncertainty (in the data available, the values for the parameters of models, the structure of the models upon which advice is based, and the ability to implement management actions). For situations in which there is considerable uncertainty, many alternative models will be compatible with the existing data so a more conservative harvest strategy is needed to satisfy the conservation-related ESD objective. As such, the MSE approach is compatible with the principles underlying the precautionary approach to fisheries management (FAO 1995). Apart from in Australia (see below), variants of the MSE approach have been applied in New Zealand (Starr *et al.* 1998), South Africa (Punt 1992; Butterworth *et al.* 1997; Cochrane *et al.* 1998), and by the Scientific Committee of the International Whaling Commission (Donovan 1989; Kirkwood 1997).

This paper first outlines the MSE approach in broad terms and how it can be used to address each of the four key questions listed above. It emphasizes the first of the four questions (evaluation of harvest strategies) because this is the most relevant to the provision of scientific advice for TAC setting, and because the answers to the other three questions are essentially byproducts of evaluating harvest strategies. Some advantages of the approach are then listed and the current use of the MSE approach in the SEF reviewed. Finally, the key challenges are identified that must be overcome in order for the MSE approach to play an even greater role in assisting with the provision of scientific advice in the SEF.

The MSE approach: an overview

The primary objective of the MSE approach is to identify, in an objective manner, the trade-offs in achieving different management objectives across a range of management options. This is the information the decision makers need to make an informed decision about management actions, given the importance they assign to each of AFMA's five

---

[2] Harvest strategies are defined here to be a combination of the rules that specify the data to be collected, the stock assessment method to be applied to those data, and the rules for how assessment results are to be used to provide a TAC (the catch control law).

legislative objectives and given that these objectives may be contradictory. The relative importance of different objectives will, of course, relate to the social, legal, and political context for each management decision. However, by basing the decision on the trade-offs among the management objectives, this context is laid bare.

Basic overview

In simple terms, the MSE approach involves evaluating the entire management system (including research programmes, stock assessment methods, performance indices and harvest strategies) by means of Monte Carlo simulation. This approach to evaluation has a long history in quantitative fisheries science (e.g. Southward 1968; Hilborn 1979; Donovan 1989).

The steps in evaluating alternative harvest strategies are as follows (Fig. 1).

- Identification of the management objectives and representation of these using a set of quantitative performance measures.
- Identification of the alternative harvest strategies.
- Development and parameterization of a set of alternative structural models (called operating models) of the system under consideration.
- Simulating the future use of each harvest strategy to manage the system (as represented by each operating model). For each year of the projection period (usually 15–25 years), the simulations involve the following four steps.
  - Generation of the data (of several types) available for assessment purposes.
  - Application of a method of stock assessment to the generated data set (including any real historical data) to determine key management related quantities and the inputs to the catch control law.
  - Application of the catch control law element of the harvest strategy to determine the TAC based on the results of the stock assessment. The catch control law may include one or more performance indicators.
  - Determination of the (biological) implications of this TAC by setting the catch for the 'true' population represented in the operating model based on the TAC. This step can include the impact of 'implementation uncertainty' (Rosenberg and Brault 1993).
- Summary of the results of the simulations by means of the performance measures and presentation of the results to the decision makers. Results are often presented as a 'decision table' showing the performance of each harvest strategy relative to each management objective.

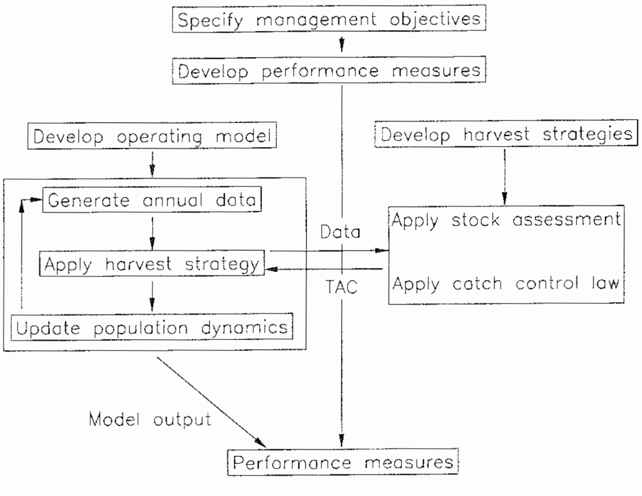


Fig. 1. Outline of the MSE approach.

The steps required to address the other three key scientific questions listed above are also based on this algorithm.

- To evaluate a stock assessment method, the performance measures need to include statistics, such as the bias or mean square error, that measure how well the stock assessment method is able to estimate key quantities of interest to management (e.g. Patterson and Kirkwood 1995).
- To evaluate the utility of a proposed performance indicator, a comparison needs to be made as to when the indicator was 'triggered' relative to when the events that it was desired to identify actually took place (e.g. Punt *et al.* 2001).
- To evaluate the value of a research programme, simulations are conducted assuming that the results of the research programme are and are not available; the differences in the values for the performance measures then reflect the 'value' of the research programme (McDonald and Smith 1997; McDonald *et al.* 1997).

Some benefits of the MSE approach

The major reason for applying the MSE approach is that it provides an objective basis for comparing alternative management actions (rules for setting TACs in the context of the SEF) in terms of their ability to satisfy the management objectives (as quantified through the performance measures). A virtue of the approach is that it allows evaluations without their direct application to the real system being managed. In several fisheries jurisdictions (e.g. Australia, New Zealand and South Africa), evaluating harvest strategies by means of simulation is often supported by both industry and conservation groups (Cochrane *et al.* 1998; Smith *et al.* 1999). The former see harvest strategies as a form of security against the machinations of the managers, and the latter gain confidence that a set of rules is in place that has been shown to perform adequately. Pre-testing of harvest strategies cannot, of course, guarantee that they will definitely work as expected in the real world. However, if a harvest strategy cannot perform adequately in the relatively ideal situations represented by the operating models, there is no reason to suspect that they will work in the real world (Sainsbury *et al.* 2000).

When based on a harvest strategy, the TAC setting process is more transparent because the rules used to set the TACs are pre-agreed and available for all interested parties to see. Having a pre-specified set of rules for setting TACs avoids problems that can arise due to over-interpretation of noisy data. Such over-interpretation can arise, for example, if, during a single year, the catch rate drops below the lowest it has ever been. The dangers of basing management decisions on essentially the last catch rate datum, as is the case for the 'CPUE strategy' in the SEF, are fairly evident. It encourages parties who desire a particular outcome in terms of TAC to place a 'spin' on the most recent catch rate (for example, artificially high because of improved technology, or artificially low because of marketing constraints). Application of the MSE approach encourages decision makers (and scientists) to focus on longer-term objectives rather than short-term considerations (Cockcroft and Payne 1999). Thus, in the SEF context, the MSE approach provides a basis for a 'think long-term, act short-term' approach to management (Francis and Shotton 1997).

Developing and parameterizing operating models can only be accomplished successfully if all participants in the assessment/management process work together. AFMA's current 'partnership' approach (Smith *et al.* 1999) integrates the views of scientists, managers and industry (and, increasingly, conservation groups) at all levels, including at the assessment group level. The process of developing operating models encourages a synthesis of available information (both quantitative and qualitative) and hence assists in the process of identifying key uncertainties and knowledge gaps.

Adoption of a harvest strategy should also lead to more efficient use of resources (Cockcroft and Payne 1999). This is because once a harvest strategy has been adopted, the time required to recommend a TAC is substantially reduced (as all that is required is to follow a pre-agreed set of steps). In principle, the additional free resources can then be directed towards addressing longer-term 'strategic' issues (Butterworth *et al.* 1997). Setting of TACs for eastern gemfish in recent years provides an example of how this potential to save time can actually be realised. For example, inputs to the stock assessment (and hence the harvest strategy) for eastern gemfish were required from five different agencies. However, given pre-agreement on the data that needed to be collected and the analyses that needed to be conducted, the most recent stock assessment was completed in less than a month (even though the stock assessment calculations themselves took two weeks of this).

The SEF and the MSE approach: the present situation

The major activities in the SEF related to the MSE approach involve the identification of performance measures by stakeholder groups, development of assessments that could form the basis for operating models, and full scale application of the MSE approach with a view towards identifying rules for setting TACs. Identification (and formal adoption) of performance measures is currently a focus at AFMA (C. Grieve, AFMA, personal communication), although there has been relatively little progress to date by the MACs and the AFMA Board in agreeing to performance measures.

Development of stock assessments

Unfortunately, the SEF does not have a particularly strong history of quantitative stock assessment that could form the basis for operating models. Before 1990, quantitative assessments were only available for tiger flathead *Neoplatycephalus richardsoni* (Montgomery 1985; Wankowski 1986), jackass morwong *Nemadactylis macropterus* (Smith 1989) and eastern gemfish *Rexea solandri* (Allen 1989). However, with the introduction of AFMA's species-specific assessment groups and occasional species-specific stock assessment workshops, the number of formal stock assessments of SEF species has recently increased markedly. For example, formal assessments are now available for blue grenadier (Punt *et al.* 2001), blue warehou, *Seriolella brama* (Punt 1999*a*), eastern gemfish (Smith and Punt 1998), eastern school whiting, *Sillago flindersi* (Punt 1999*b*), and orange roughy, *Hoplostethus atlanticus* (CSIRO and TDPIF 1996), and assessments are currently being developed for ling, *Genypterus blacodes*, and spotted warehou, *Seriolella puncata* (R. Thomson, CSIRO Marine Research, personal communication).

Recent SEF assessments based on integrated analysis (Fournier and Archibald 1982; Methot 1989, 1990) (Table 1) and the assessments of school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus* (Punt 2000; Punt *et al.* 2000) have been conducted by species-specific subgroups that include scientists who do not come from a modelling background, industry and managers. In some cases, conservation groups are also represented on species assessment groups. The broader representation at the assessment group level has lead to wider consideration of uncertainty, in particular, uncertainty regarding model structure. For example, the recent assessment of school shark (Punt *et al.* 2000) considered the implications of stock structure within Australia as well as those of movement of school sharks from New Zealand to Australia. A broader range of hypotheses is usually considered when conducting MSE than would be normal when conducting a stock assessment (e.g. allowing for depensation in the stock-recruitment relationship). This is because, although two alternative hypotheses may fit the existing assessment data equally well, they may have quite different consequences when projected into the future. Although examining a wide range of alternative hypotheses is an advantage of the MSE approach, the lack of constraint on hypotheses can lead to management decisions being based on highly unlikely (but highly consequential) hypotheses (Butterworth *et al.* 1996).

Implementation of the full MSE approach

To date, the full MSE approach has been applied to three species in the SEF: orange roughy, blue grenadier and the eastern stock of gemfish. For blue grenadier, the MSE approach has been used only to evaluate the value of research programmes. Punt (1999*c*) examined the implications of changing the amount of sampling of discards through the Integrated Scientific Monitoring Programme (Smith *et al.* 1997) in terms of the ability to estimate year-class strength for blue grenadier. However, the use of the MSE approach for orange roughy and eastern gemfish has progressed to the evaluation of rules for setting TACs.

Although MSE studies based on orange roughy were conducted as early as 1991 (e.g. Smith 1993), the results of these studies have not been implemented[3]. There are two reasons for this 'failure to implement'. First, the work was not undertaken as part of a stock assessment group process, but as an independent scientific investigation focused on methods development. Second, the work was undertaken early in the development of the fishery, and before an agreed stock assessment was available. This agreed assessment did not emerge until several years later, at which time explicit strategies *were* put in place to sequentially reduce catches to 'sustainable' levels. These strategies comprised fixed-TAC situations rather than feedback harvest rules, and were evaluated by projecting different future sequences of catches with the basic stock assessment model, to achieve acceptable levels of risk.

The assessment of eastern gemfish (Smith and Punt 1998) indicates that the stock is currently overexploited, recruitment has been poor for a decade, and the stock is well below the limit reference point set by AFMA. The targeted TAC for the fishery is currently zero, although allowance is made for the landing of incidental bycatch. The MSE approach has been used to identify rules for setting TACs that allow targeted catches if there is evidence for some recovery, yet keep catches as low as possible if there are no signs of recovery. The situations considered in the evaluation have examined uncertainty about *inter alia* the level of historical catches, the form of the stock-recruitment relationship (e.g. is the relationship depensatory/are the residuals auto-correlated), whether selectivity is density-dependent, and the relationship between catch rates and abundance (Punt and Smith 1999). Rules for setting TACs based on Virtual Population Analysis and a surplus production model have been considered and the performance of each candidate rule has been evaluated with several measures of risk to the resource (Punt and Smith 1999). Outcomes from this modelling have included a refinement of the agreed reference point for the resource and a better (and less confrontational) approach to stock assessment and TAC setting for this species.

The SEF and the MSE approach: key challenges

We see four key challenges to the successful implementation of the MSE approach in the SEF (and elsewhere): selection of appropriate objectives and performance measures, the complexity of the approach, the selection of the hypotheses to consider and their relative weights, and the extension to examine the implications of management decisions on non-target species and the ecosystem.

The most common problem when applying fisheries risk assessment methods is the selection of appropriate performance measures (Butterworth *et al.* 1997; Francis and Shotton 1997; Butterworth and Punt 1999). In particular, few MSE/risk assessment frameworks have integrated biological with economic considerations (Baldursson *et al.* (1996) is a notable exception), generally quantifying the effect of management decisions on industry in terms of discounted total catches. Quantification of 'risk' has also proved problematic. It is clear that there must be a level of biomass below which effects such as stock collapse, species replacement, depensatory processes, or ecosystem effects will occur. However, there are currently few studies that could be used to select this level for marine fish species[4]. This has meant that 'risk' has most often been defined as the probability of dropping below some largely arbitrary biomass (e.g. 20% of the virgin biomass).

The MSE framework (Fig. 1) is difficult to communicate to non-experts. Even fisheries biologists with many years' experience have found the MSE approach difficult to understand because it is quite different from conventional approaches to fisheries stock assessment. This communication problem is further compounded by a large amount of (admittedly confused) nomenclature (Smith *et al.* 1999). Our experience is that it is relatively straightforward to convince stock assessment group participants of the benefits of adopting the MSE approach. However, to date little time has been spent informing the Management Advisory Committees of these benefits.

---

[3] However, limit reference points have been defined for this species, and formal assessments used in setting TACs are available for several stocks.

[4] Exceptions include Myers *et al.* (1994) who examined risks of recruitment failure and Liermann and Hilborn (1997) who developed probability distributions for depensation.

It is acknowledged (Lyle 1998) that there is a shortage of stock assessment scientists in Australia. The lack of skills is even greater for MSE because the complexity and computational requirements of the evaluation process are substantially greater than required to conduct a standard stock assessment. For example, the operating model currently being used to compare alternative harvest strategies for a range of SEF species includes *inter alia* modules for the selectivity function, the growth model, the recruitment function and the relationship between fishing effort and fishing mortality. Each of these modules has many options (e.g. selectivity can be density-dependent and allowance needs to be made for differences between the selectivity pattern for the landed catch and that for the discards). The lack of skills is overcome to some extent by the fact that applying a harvest strategy does not require considerable knowledge of stock assessment methodology and, in fact, adoption of a harvest strategy could negate the need for a detailed annual stock assessment process for species for which harvest strategies have been agreed.

Consideration of a broader range of hypotheses necessitates a determination of the relative plausibility of each hypothesis when comparing alternative harvest strategies. To date, the process of evaluating plausibility has been to exclude 'clearly implausible' scenarios and to give the remaining scenarios equal weight. Unfortunately, members of assessment (and management) groups may differ in terms of what they regard as plausible/implausible and much more work is needed in this area (e.g. Butterworth *et al.* 1996). Of particular concern is if a participant's assessment of the implausibility of a scenario is determined by the TACs it implies. In some sense, therefore, if care is not taken to avoid it, moving to an MSE approach may simply move the arguments, from being about the data and model assumptions used in assessment, to being about the hypotheses on which the selection of the harvest strategy is based.

The question of plausibility also relates directly to the different decision makers' attitudes to risk and uncertainty. Some decision makers may be willing to accept more risk when uncertainty is high (and 'things could be better than they may look'), whereas other decision makers demand a much more conservative management approach in the face of increased uncertainty. This last issue is evident when objectives are chosen. Although the MSE approach is designed to encourage a long-term approach to decision making, it is possible to over-emphasize short-term considerations by, for example, using a high discount rate in catch-related performance measures.

All of the applications of the MSE approach in the SEF have considered the effects of management actions on the target species. There is no conceptual reason why the MSE approach cannot be applied to examine the ecosystem implications of management actions (Sainsbury *et al.* 2000). For example, Maunder *et al.* (2000) examine the implications of different rules for controlling by-catch of New Zealand sea lions by the fishery for arrow squid off southern New Zealand on both the sea lion population and the squid fishery. However, lack of sufficient data combined with a poor understanding of the underlying processes has precluded work to date in the area of ecosystem effects in the SEF with the MSE approach. Understanding the implications of technical interactions (Pikitch 1991) among fisheries is simpler and work is currently underway to examine the effects of these interactions for four species in the South East Fishery (A. E. Punt, unpublished).

The SEF and the MSE approach: the future

Table 1 provides information on the assessment status of the 16 SEF quota species (separate entries are provided for eastern and western gemfish, which are treated separately in the quota system). Assessments based on integrated analysis are available for five 'species' and planned or under development for another three. Except for eastern school whiting, the formal assessments have formed the basis for population projections. There are currently no quantitative assessments for nine of the 17 'species' in Table 1. The likelihood of formal assessments being conducted for six of these (john dory, mirror dory, ocean perch, red royal prawn, silver trevally and western gemfish) is low as they are not 'priority' species, and resources for stock assessment are limited. Quantitative assessments for these species would also be constrained because the only assessment data available, apart from landings information, are catch rates and some length–frequency data. Given adequate resources it should be possible to conduct age-based assessments for both flathead and morwong. Harvest strategies for four of the species in Table 1 are currently being examined (Cui, unpublished). However, this examination is based on generic considerations and the four species are included primarily as example species.

Table 1 appears to indicate that there has been little progress towards adopting an MSE approach in the SEF even though AFMA and many of the species-specific assessment groups strongly support such adoption. However, it should be borne in mind that, as recently as 1994, formal assessments were available for only two SEF species (orange roughy and eastern gemfish) and projections for only the first of these. Considerable progress has been made towards developing formal stock assessments for those species for which this is likely to be feasible, so the basis for a formal evaluation of harvest strategies for several SEF species should be available soon. It is likely that the full MSE approach could be applied now to species such as blue grenadier for which assessments are available and consideration has already been given by the assessment group to alternative structural assumptions.

Selection of appropriate objectives and performance measures and methods for weighting alternative hypotheses remain, to some extent, outside the scientific realm (particularly the former). Successful implementation of the MSE approach to evaluate harvest strategies, performance indicators, stock assessment methods and research programmes will therefore require that stakeholders are willing to commit time and resources to a process for resolving these problems in addition to providing continued support for stock assessment work.

Acknowledgment

Robin Thomson is thanked for his comments on an earlier version of this paper.

References

Allen, K. R. (1989). A cohort analysis of the gemfish stock of southeast Australia. Document submitted to the 29 November 1989 meeting of the Demersal and Pelagic Fish Research Group.

Baldursson, F. M., Danielsson, A., and Steffanson, G. (1996). On the rational utilization of the Icelandic cod stock. *ICES Journal of Marine Science* **53**, 643–58.

Butterworth, D. S., and Punt, A. E. (1999). Experiences in the evaluation and implementation of management procedures. *ICES Journal of Marine of Science* **56**, 985–98.

Butterworth, D. S., Cochrane, K. L., and De Oliveira, J. A. A. (1997). Management procedures: A better way to manage fisheries? The South African experience. In 'Global trends: Fisheries management'. (Eds E. L. Pikitch, D. D. Huppert and M. P. Sissenwine.) pp. 83–90. (American Fisheries Society: Bethesda.)

Butterworth, D. S., Punt, A. E., and Smith, A. D. M. (1996). On plausible hypotheses and their weighting, with implications for selection between variants of the Revised Management Procedure. *Reports of the International Whaling Commission* **46**, 637–40.

Cochrane, K. L., Butterworth, D. S., De Oliveira, J. A. A., and Roel, B. A. (1998). Management procedures in a fishery based on highly variable stocks and with conflicting objectives: Experiences in the South African pelagic fishery. *Reviews in Fish Biology and Fisheries* **8**, 177–214.

Cockcroft, A. C., and Payne, A. I. L. (1999). A cautious fisheries management policy in South Africa: the fisheries for rock lobster. *Marine Policy* **23**, 587–600.

CSIRO and TDPIF (1996). Orange roughy 1994, Stock assessment report, South East Fishery Assessment Group (Australian Fisheries Management Authority: Canberra.)

Donovan, G. P. (1989). The Comprehensive Assessment of Whale Stocks: The Early Years. *Reports of the International Whaling Commission* (*Special Issue* 11).

FAO. (1995). Precautionary approach to fisheries. Part 1: Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Fisheries Technical Paper No. 350/1.

Fournier, D., and Archibald, C. P. (1982). A general theory for analyzing catch at age data. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1195–207.

Francis, R. I. C. C., and Shotton, R. (1997). "Risk" in fisheries management: A review. *Canadian Journal of Fisheries and Aquatic Science* **54**, 1699–715.

Hilborn, R. (1979). Comparison of fisheries control systems that utilize catch and effort data. *Journal of the Fisheries Research Board of Canada* **36**, 1477–89.

Kirkwood, G. P. (1997). The revised management procedure of the International Whaling Commission. In 'Global Trends: Fisheries Management'. (Eds E. L. Pikitch, D. D. Huppert and M. P. Sissenwine.) pp. 91–9. (American Fisheries Society: Bethesda.)

Liermann, M., and Hilborn, R. (1997). Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Science* **54**, 1976–84.

Lyle, J. (1998). Providing stock assessments for Australia fisheries, Australian Society for Fish Biology. (Tasmanian Aquaculture and Fisheries Institute: Hobart, Australia.)

Maunder, M. N., Starr, P. J., and Hilborn, R. (2000). A Bayesian analysis to estimate loss in squid catch due to the implementation of a sea lion population management plan. *Marine Mammal Science* **16**, 413–26.

McDonald, A. D., and Smith, A. D. M. (1997). A tutorial on evaluating expected returns from research for fishery management. *Natural Resource Modelling* **10**, 185–216.

McDonald, A. D., Smith, A. D. M., Punt, A. E., Tuck, G. N., and Davidson, A. J. (1997). Empirical evaluation of expected returns from research on stock structure for determination of total allowable catch. *Natural Resource Modelling* **10**, 3–29.

Methot, R. (1989). Synthetic estimates of historical abundance and mortality for northern anchovy. *American Fisheries Society Symposium* **6**, 66-82.

Methot, R. (1990). Synthesis model: an adaptable framework for analysis of diverse stock assessment data. *Bulletin of the International North Pacific Fisheries Commission* **50**, 259–77.

Montgomery, S. S. (1985). Aspects of the biology of the tiger flathead *Playcephalus richardsoni* and the associated fishery. MSc Thesis, University of New South Wales, Australia.

Myers, R. A., Rosenberg, A. A., Mace, P. M., Barrowman, N., and Restrepo, V. R. (1994). In search of thresholds for recruitment overfishing. *ICES Journal of Marine Science* **51**, 191–205.

Patterson, K. R., and Kirkwood, G. P. (1995). Comparative performance of ADAPT and Laurec–Shepherd methods for estimating fish population parameters and in stock management. *ICES Journal of Marine Science* **52**, 183–96.

Pikitch, E. K. (1991) Use of a mixed species yield-per-recruit model to explore the consequences of various management policies for the Oregon flatfish fishery. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 349–59.

Punt, A. E. (1992). Selecting management methodologies for marine resources, with an illustration for southern African hake. *South African Journal of Marine Science* **12**, 943–58.

Punt, A. E. (1999*a*). An assessment of blue warehou for 1999 based on integrated analysis. Document submitted to the 7–8 June 1999 meeting of BWAG. (Australian Fisheries Management Authority: Canberra.)

Punt, A. E. (1999*b*). ADAPT and integrated analysis assessments of school whiting. Document submitted to the 17-18 June 1999 school whiting workshop. (Australian Fisheries Management Authority: Canberra.)

Punt, A. E. (1999*c*). Evaluating the costs and benefits of alternative monitoring programmes for fisheries management. In 'Proceedings of the International Conference on Integrated Fisheries Monitoring, Sydney, Australia. 1–5 February 1999'. (Ed. C. P. Nolan.) pp. 209–22. (FAO: Rome.)

Punt, A. E. (2000). Assessment of the population of gummy shark (*Mustelus antarcticus*) in Bass Strait. SharkFAG Document SharkFAG/00/D2. (Australian Fisheries Management Authority: Canberra.)

Punt, A. E., and Smith, A. D. M. (1999). Harvest strategy evaluation for the eastern stock of gemfish (*Rexea solandri*). *ICES Journal of Marine of Science* **56**, 860–75.

Punt, A. E., Campbell, R. A., and Smith, A. D. M. (2001). Evaluating empirical indicators and reference points for fisheries management:

application to the broadbill swordfish fishery off eastern Australia. *Marine and Freshwater Research* **52**, 819–32.

Punt, A. E., Pribac, F., Walker, T. I., Taylor, B. L., and Prince, J. D. (2000). Stock assessment of school shark *Galeorhinus galeus* based on a spatially-explicit population dynamics model. *Marine and Freshwater Research* **51**, 205–20.

Punt, A. E., Smith D. C., Thomson, R. B., Haddon, M., He, X., and Lyle, J. (2001). Stock assessment of the blue grenadier *Macruronus novaezelandiae* resource off south-eastern Australia. *Marine and Freshwater Research* **51**, 701–17.

Rosenberg, A. A., and Brault, S. (1993). Choosing a management strategy for stock rebuilding when control is uncertain. In 'Risk Evaluation and Biological Reference Points for Fisheries Management'. (Eds S. J. Smith, J. J. Hunt and D. Rivard.) pp. 243–9. *Canadian Journal of Fisheries and Aquatic Sciences* (*Special Publication*) **120**.

Sainsbury, K. J., Punt, A. E., and Smith, A. D. M. (2000). Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science* **57**, 731–41.

Smith, A. D. M. (1993). Risks of over- and under-fishing new resources. In 'Risk Evaluation and Biological Reference Points for Fisheries Management'. (Eds S. J. Smith, J. J. Hunt and D. Rivard.) pp. 261–7. *Canadian Journal of Fisheries and Aquatic Sciences* (*Special Publication*) **120**.

Smith, A. D. M. (1994). Management strategy evaluation – the light on the hill. In 'Population Dynamics for Fisheries Management. Australian Society for Fish Biology Workshop Proceedings, Perth, 24–25 August 1993'. (Ed. D. A. Hancock.) pp. 249–53. (Australian Society for Fish Biology: Perth.)

Smith, D. C. (1989). The fisheries biology of jackass morwong (*Nemadactylus macropterus* Block and Schneider) in southeastern Australian waters. PhD Thesis, University of New South Wales, Australia.

Smith, A. D. M., and Punt, A. E. (1998). Stock assessment of gemfish (*Rexea solandri*) in eastern Australia using maximum likelihood and Bayesian methods. In 'Fisheries Stock Assessment Models' (Eds T. J. Quinn II, F. Funk, J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan and C-I Zhang.) pp. 245–86. (Alaska Sea Grant College Program, AK-SG-98-01: Fairbanks.)

Smith, A. D. M., Sainsbury, K. J., and Stevens, R. A. (1999). Implementing effective fisheries management systems – management strategy evaluation and the Australian partnership approach. *ICES Journal of Marine Science* **56**, 967–79.

Smith, D. C., Gilbert, D. J., Gason, A., and Knuckey, I. A. (1997) Design of an integrated scientific monitoring program for the South East Fishery. (Australian Fisheries Management Authority: Canberra.)

Southward, G. M. (1968). A simulation of management strategies in the Pacific halibut fishery. *International Pacific Halibut Committee Scientific Report* **47**, 1–70.

Starr, P. J., Breen, P. A., Hilborn, R. H., and Kendrick, T. H. (1997). Evaluation of a management decision rule for a New Zealand rock lobster substock. *Marine and Freshwater Research* **48**, 1093–101.

Tilzey, R. D. J. (1999). The South East Fishery 1998. Fishery Assessment Report compiled by the South East Fishery Assessment Group. (Australian Fisheries Management Authority: Canberra.)

Wankowski, J. W. (1986). Surplus yield estimates for the eastern Bass Strait demersal trawl fishery: 3. Tiger flathead. Marine Science Laboratory Technical Report No. 53.

Manuscript received 21 December 1999; revised and accepted 5 May 2000

Biology and life history parameters

Quantitative stock assessment

Marine and Freshwater Research

Contents Volume 52 Number 4 2001

A complex quota-managed fishery: science and management in Australia's South East Fishery

The fishery and its management

The South East Fishery ecosystem

(continued inside back cover)

FISHERIES
RESEARCH &
DEVELOPMENT
CORPORATION

1323-1650(2001)52:8;3-A

ISSN 1323-1650