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State Government Victoria Department of Primary Industries

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Fisheries Research and Development Corporation

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NON-TECHNICAL SUMMARY

2002/033 Rapid assessment of sustainability for ecological risk of shark and other chondrichthyan bycatch species taken in the Southern and Eastern Scalefish and Shark Fishery

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Objectives:

1. Quantitatively categorise bycatch species of shark and other chondrichthyans taken in the GHATF, SETF, and GABTF based on 'relative biological productivity'.
2. Semi-quantitatively categorise chondrichthyan bycatch species taken in these fisheries based on 'catch susceptibility' determined from availability, encounterability, selectivity, and post-capture mortality to the fishery based on presently available data.
3. Semi-quantitatively determine diets of chondrichthyan bycatch species taken in these fisheries from analysis of stomach contents analyses to contribute to establishing their positions in marine food chains.
4. Resolve taxonomic uncertainties of various chondrichthyan species, particularly uncertainties among dogfish species.
5. Undertake assessment of sustainability for ecological risk of each chondrichthyan bycatch species through the application of rapid assessment techniques developed through the AFMA funded project titled 'Ecological Risk Assessment for Australian Commonwealth Fisheries'.
6. Address the sustainability and ecological risk of endeavour dogfish, Harrison's dogfish, southern dogfish and other dogfish species with high priority.

Non Technical Summary:

Management of bycatch and byproduct species requires different types of research, survey, and monitoring information than currently adopted for high value target species. It is not practical to collect the extensive data required for stock assessment of individual species; there are far too many species to address. Furthermore, management decisions need to be made long before the required data sets for full assessment can be collected. Because of the comparatively low biological productivity of chondrichthyan species (sharks, rays and holocephalans), their populations can be depleted in a shorter period than it takes to collect sufficiently long time-series of data to undertake reliable stock assessments. Alternative rapid assessment methods are therefore required.

Assessment of the sustainability of each chondrichthyan species in southern Australia was undertaken through rapid assessment of ecological risk from effects of fishing using a framework involving five components. This involved combining the results for three components determined by the present project with the results for two components determined by a separate project. The three components determined by the present project are biological productivity (Objective 1), catch susceptibility (Objective 2), and food web

trophic position (Objective 3), and the two components determined by FRDC Project 2000/007 are catch (proxy for relative abundance across the SESSF) and relative abundance trend. While all five components apply to each species, catch susceptibility applies to each fishing method.

Maximum age and reproductive output were adopted as proxies for biological productivity. Several methods were adopted for ageing chondrichthyan species using vertebrae or dorsal fin-spines, present only in dogfish (Squaliformes), horn sharks (Heterodontiformes), and holocephalans (Holocephaliformes). The vertebrae do not calcify and form visible bands in sixgill and sevengill sharks (Hexanchiformes) or angel sharks (Squatiniformes) and, therefore, cannot be aged. New methods were developed for ageing the Port Jackson shark (*Heterodontus portusjacksoni*), holocephalans, catsharks, and dogfishes. Species of dogfish, catsharks and carpet sharks (Orectolobiformes), and electric rays (Torpediniformes) were very difficult to age and although some species were successfully aged as part of the present study, adequate methods were not developed for several other species.

The longest-lived species are the dogfishes and holocephalans and are classed at very high risk; they can withstand only very limited additional mortality, indicative of low biological productivity. Generally at high risk are the catsharks, carpet sharks, and wobbegongs (Orectolobiformes), mackerel and thresher sharks (Lamniformes), and horn sharks (Heterodontiformes). No species were classed as low risk, but the species generally classed at medium or medium–high risk are the whaler, hammerhead, and smoothhound sharks (Carcharhiniformes), sawsharks (Pristiophoriforrmes), skates (Rajiformes), and eagle devil rays, stingrays, and stingarees (Myliobatiformes).

In the present study, only sharks occupy trophic positions >4.25 classed as high risk (11 species); most shark species occupy a trophic position ranging 4.00–4.25 classed as medium risk (33 species), with a few species occupying a trophic position <4.00 classed low risk (5 species). Rays mostly occupy trophic positions classed as low risk (17 species), with a few species classed as medium risk (5 species). All holocephalans occupy trophic positions classed as low risk (6 species), with the exception of a single species classed as medium risk.

Taxonomic uncertainties of several species of the genera *Centrophorus*, *Squalus*, and *Orectolobus* were resolved. Only three gulper shark species (*Centrophorus* spp) occur in Australia: Harrisons dogfish (*C. harrissoni*), southern dogfish (*C. zeehani*), and endeavour dogfish (*C. moluccensis*). *Centrophorus squamosus* and *C. uyato* are no longer recognised as species for Australia. Green-eye spurdog previously named *Squalus mitsukurii* is renamed *Squalus chloroculus* as an Australian endemic species and spikey spurdog (*Squalus megalops*) may be represented by more than one species in Australia. The two wobbegong species *Orectolobus ornatus* and *O. maculates* had been recognised for temperate eastern Australia, but it had been considered that other closely related species might also be present. The subspecies *O. ornatus halei* in southern Australia and *O. ornatus ornatus* in north-eastern waters had been distinguished but remained unresolved until recently when sufficient research material became available to describe *O. ornatus* (De Vis) and *O. halei* Whitley. *Orectolobus ornatus* occurs from Port Douglas in Queensland to Sydney in New South Wales, whereas *O. halei* occurs from Southport in Queensland around the southern coast to Norwegian Bay in Western Australia. In addition to the goblin shark (*Mitsukurina owstoni*), there is evidence of another species in the genus *Mitsukurina*.

Species at highest risk are those that also have other high risk factors. A total of 23 species were identified at high risk under catch susceptibility and 13 are also at high risk from other factors. These species belong to the order Hexanchiformes (1 species from automatic longline), Squaliformes (7 species from otter trawl of which 3 are also from automatic longline), Pristiophoriformes (1 species from shark gill net), Squatiniformes (1 species from otter trawl), Carcharhiniformes (3 species from shark gillnet), and Holocephaliformes (8 species from otter trawl and 1 from shark gillnet).

Three species of gulper shark (*C. harrissoni*, *C. moluccensis*, and *C. zeehani*) and greeneye spurdog (*Squalus chloroculus*) are at highest risk from the effects of fishing because of their low biological productivity and abundance trend. In addition, *C. harrissoni* is now rare and *S. chloroculus* has high trophic level. Three other dogfish—prickly dogfish (*Oxynotus bruniensis*), bareskin dogfish (*Centroscyllium kamoharai*), and longsnout dogfish (*Deania quadrispinosa*)—are likely to have low biological productivity, and *C. kamoharai* is rare. School shark (*Galeorhinus galeus*) and all holocephalans have low biological productivity and four of the holocephalan species—black ghostshark (*Hydrolagus* sp A), giant ghostshark (*Hydrolagus* sp C), bigspine spookfish (*Harriotta raleighana*), and Pacific spookfish (*Rhinochimaera pacifica*)—are rare. The closure of waters >700 m will provide for improved management of many species of dogfish and holocephalans, but will provide little benefit to the gulper sharks and greeneye spurdog, which inhabit the upper- and mid-slope. The upper- and mid-slope species will receive benefit from implementation of closed areas.

OUTCOMES ACHIEVED

The present report provides a comprehensive collation of results relevant to rapid assessment of sustainability for ecological risk of sharks, rays and holocephalans in southern Australia. The present study complements a similar study titled 'Northern Australian sharks and rays: the sustainability of target and bycatch species, Phase 2' (FRDC 2002/064) (Salini *et al.* 2007). The present collation includes results from the present project and results from 'Shark and other chondrichthyan byproduct and bycatch estimation in the Southern and eastern Scalefish and Shark Fishery' (FRDC Project 2001/007) (Walker and Gason 2007) and several other FRDC projects. The results are presented in a framework that builds on the approach developed as part of the CSIRO-run project titled 'Ecological risk assessment for Australian Commonwealth fisheries' (AFMA R01/0934 and AFMA R04/1072).

The results have been presented variously in unpublished internal reports and oral presentations to AFMA, industry, SharkRAG, DAG, GHATMAC, SETMAC, CSIRO, and various scientific forums. The results provide key data inputs to development of Management Plans and extensive legislation on the SESSF for quota baskets, trip limits, trigger limits, closed areas, and depth exclusions, implemented in response to the Ministerial Direction to AFMA of December 2005 to manage the broader environmental impacts of fishing.

The results will continue to contribute to documentation requirements for several important ongoing processes prescribed in legislation and national policies.

(a) Strategic assessment of fisheries prescribed under the Australian Environment Protection and Biodiversity Conservation Act 1999. AFMA has previously used other data sets for this purpose, but the present report and associated outputs will serve to update and refine the documentation.

(b) Bycatch Action Plans prescribed under the Australian Fisheries Act 1991. The present report and associated outputs will serve to update and refine the documentation.

(c) Australia's National Plan of Action for the Conservation and Management of Sharks launched 26 May 2004. The present report provides required information to the Shark Plan Implementation Committee for updating the Shark Assessment Report, submitted periodically to the FAO Committee of Fisheries.

The new approaches to rapid assessment of sustainability for ecological risk developed or applied through the present project have been presented at various forums in Australia, New Zealand, USA, Brazil, Chile, Ecuador, Mexico, Taiwan, Philippines, Palau, and Marshall Islands where they have been extremely well received. Both FAO and IUCN have shown great interest in the approach.

A major outcome is that, from the present project and related projects, there is now a firm body of data on chondrichthyan species from throughout Australia. These data are readily accessible and can be applied to address issues related to the management of chondrichthyan fauna as they arise. These projects provide a legacy of a large group of trained young scientists in Australia with specialist skills in chondrichthyan biology and collaborative partnerships that continue to address issues related to fisheries management.

Keywords: SESSF, catch susceptibility, biological productivity, trophic level

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Species names were based on the Codes for Australian Aquatic Biota (www.marine.csiro.au/caab/caabsearch).

FINAL REPORT

2002/033 Rapid assessment of sustainability for ecological risk of shark and other chondrichthyan bycatch species taken in the Southern and Eastern Scalefish and Shark Fishery

Background

Acronyms

AFMA	Australian Fisheries Management Authority
BRS	Bureau of Rural Sciences
CSIRO	CSIRO Marine and Atmospheric Research
DAFF	Department of Agriculture Fisheries and Forests
DAG	Deepwater Assessment Group
DEWR	Department of Environment and Water Resources
FIRTA	Fishing Industry Research Trust Account
FRDC	Fisheries Research and Development Corporation
GABRAG	Great Australian Bight Resource Assessment Group
GABTF	Great Australian Bight Trawl Fishery
GHATF	Gillnet Hook and Trap Fishery
IPOA-Sharks	International Plan of Action for the Conservation and Management of Sharks
ISMP	Integrated Scientific Monitoring Program
NPOA-Sharks	National Plan of Action for the Conservation and Management of Sharks
MAFFRI	Marine and Freshwater Fisheries Research Institute
SAG	Shark Assessment Group
SESSF	Southern and Eastern Scalefish and Shark Fishery
SETF	South East Trawl Fishery
SETRAG	South East Trawl Resource Assessment Group
SharkRAG	Southern Shark Resource Assessment Group
SIRC	Shark Implementation and Review Committee

Structure of report

The report has all the prescribed sections of a standard FRDC report and each of the Methods section and the Results/Discussion section has inter alia sub-sections related to each of the six project objectives. The sub-sections addressing the objectives are biological productivity (Objective 1), catch susceptibility (Objective 2), diet (Objective 3), taxonomic uncertainty (Objective 4), ecological risk assessment (Objective 5), and sustainability of dogfish (Objective 6). Data summaries are provided as tables and figures in the main body of the report and the comprehensive information is presented in appendices. Information in the appendices include information on intellectual property (Appendix 1), staff and postgraduate students undertaking the present project (Appendix 2), extension strategy (Appendix 3), press release prepared at the beginning of the project (Appendix 4), data management procedures (Appendix 5), list of outputs from project (relevant scientific papers and presentations) (Appendix 6), scientific journal papers published (Appendices 7a–3p), scientific journal papers in press (Appendices 8a–8c), journal papers submitted (Appendices 9a–9c), and a book chapters published (Appendices 10a).

Conduct of present project

The present project was designed to meet various requirements of Australia's National Plan of Action for the Conservation and Management of Sharks (NPOA-Sharks) developed by the national Shark Assessment Group (SAG). Australia's NPOA-Sharks consists of a Shark Assessment Report and Shark Plan ratified by appropriate government ministers for the Commonwealth and all States and Territories and launched on 26 May 2004. The Shark Plan triggers various management actions to be fulfilled within time-frames of 1, 2, 3, and 5 years. Progress applying the Shark Plan is monitored by the Shark Implementation and Review Committee (SIRC), which reports to Marine and Coastal Committee.

The present project provides data for ongoing risk assessment of chondrichthyan species. In combination with monitoring and distributional data on target, byproduct and bycatch chondrichthyan species from shark surveys in the shark gillnet sector of the GHATF and the Integrated Scientific Monitoring Program in the SETF and GABTF, data from the present project provide the necessary data for future development of broad-scale ecosystem models for southern Australia. For this purpose, based on relative catches of bycatches from the Shark Gillnet Sector and Shark Hook Sector of the GHATF identified by FRDC Project 1999/103 (Walker and Hudson 2005b; Walker *et al.* 2005b) and from the GHATF, SETF, and GABTF identified by FRDC Project 2000/007 (Walker and Gason 2007), the most abundant species were intensively sampled through the present project. This was to ensure that robust demographic parameter estimates for the most abundant species are available for future ecosystem modelling and monitoring.

The present project was undertaken as a collaborative project between the Marine and Freshwater Fisheries Research Institute (MAFFRI), CSIRO Marine and Atmospheric Research (CSIRO), University of Melbourne, Deakin University, University of Adelaide, University of Tasmania, Macquarie University, and the University of Indiana (Appendix 2). There was significant input from SharkRAG.

The Principal Investigator and Co-Investigator were participants on the ERA Project. In addition, these investigators and the staff employed on the project together have special expertise in shark biology, chondrichthyan taxonomy, genetics, and a long track-record in assessment of shark and other chondrichthyan populations, investigation of gear selectivity, and identification and analysis of stomach contents of these species. Through MAFFRI, CSIRO, and SharkRAG, the project staff will have appropriate input from specialist shark modellers, fishery managers, and shark fishers.

Several initiatives have been taken to ensure close alignment between the present project and FRDC Project Proposal 2002/064 titled 'Northern Australian sharks and rays: the sustainability of target and bycatch species, Phase 2'. One is for the Principal Investigator of each of the two projects to serve as a Co-Investigator on the other project. Another major initiative is for the national Shark Assessment Group (SAG), established to develop the Australian National Plan of Action for the Conservation and Management of Sharks, to serve as a steering committee for both projects. Each year, the Principal Investigator from the Southern Australian Project Team met with members of the Northern Australian Project Team.

To ensure all collaborators collected common data and understood the methods of analysis, since June 2003, five project-workshops, each up to about 1-week duration, were held at the MAFFRI Queenscliff Centre. These workshops were attended by 12–35 scientists and were increasingly seen as valuable learning experiences and were attended by scientists outside the project, including scientists from all states in Australia, South Africa, UK and USA. Initially the workshops involved discussing sampling, operational and methodology issues, but subsequently were increasingly directed to data analysis and interpretation, and peer review of work.

The first workshop (16–20 April 2003) was attended by 12 team project collaborators (5 MAFFRI staff and 7 postgraduate students) based in Queenscliff, Adelaide, and Melbourne. The second workshop (18–22 April 2003) was attended by the same participants of the first workshop, plus one person from CSIRO, and two postgraduate students from Hobart (15 people). Much of the time at the first two workshops involved dissection of sharks, rays, and chimaeras to ensure all collaborators adopted a common approach to dissection, interpretation of material, and data collection. The third workshop (15–19 December 2003) focussed on data management and data analysis using the statistical package SAS. The participants included, in addition to 5 staff from MAFFRI, and 12 postgraduate students from Melbourne, Deakin, Monash, Adelaide, Tasmania and Macquarie Universities (17 people in total). The fourth workshop, held 5–8 April 2004, focused `on exchanging information on ageing techniques and appropriate analysis of data for sharks, rays, and holocephalans. The 23 participants included staff from MAFFRI, CSIRO, Melbourne Aquarium, IUCN Shark Specialist Group, and academics and postgraduate students from the Universities of Melbourne, Deakin, Monash, Adelaide, Tasmania, Macquarie, Queensland, and Murdoch; two were international participants. The fifth workshop, held during 7–9 March 2005, focused on the complexities and peculiarities of chondrichthyan reproduction. Interest in the subject attracted 35 participants from CSIRO (1), SARDI (1), NSW Fisheries (1), Melbourne Aquarium (4), St Vincent's Institute of Medical Research (1), and Universities of Indiana (1), Deakin (4), Melbourne (6), Monash (3), Adelaide (1), Tasmania (1), Macquarie (1), Newcastle (2), Murdoch (2), and Queensland (5). Key presenters at the workshop were Professor William C. Hamlett, Professor David Galloway, and Terry Walker.

In addition, project staff met with the on-board observers participating in the Integrated Scientific Monitoring Program to provide taxonomic advice for improving species identifications. The Principal Investigator and Co-investigator attended meetings of the Northern Australian Shark Project (FRDC Project 2002/064) (Salini *et al.* 2007) to ensure alignment between the projects of southern and northern Australia to provide a national approach.

Previous and other research

Previous research of sharks in the GHATF shark gillnet sector of the SESSF focused on gummy shark (*Mustelus antarcticus*), school shark (*Galeorhinus galeus*), common sawshark, southern sawshark, and elephant fish during 1973–76 and 1986–87, and 1990–01. This research investigated reproduction, morphometrics, gillnet selectivity, age and growth, and movement to determine all the basic fisheries population parameters required for stock assessment of these species.

The earlier biological data came from several projects: 'Investigations of the Gummy Shark from South-eastern Australian waters' (FIRTA Project 1973–76), Southern Shark Assessment (FIRTA Project 1985–88), 'Southern Shark Tagging' (FRDC Project 93/066), and 'Southern Shark Tag Database' (FRDC Project 96/162). In addition to the present project, available byproduct and bycatch data are from the FIRTA 1973–76 Project and the 'Pilot Fixed Site Station Survey (AFMA Project 1998). Other closely related projects include the 'Saw Shark, Elephant Fish and By-catch Evaluation in the Southern Shark Fishery' (FRDC Project 99/103), the 'Shark and other chondrichthyan byproduct and bycatch estimation in the Southern and Eastern Scalefish and Shark Fishery' (FRDC Project 2000/007), and 'Catch analysis and productivity of deepwater dogfish resource in southern Australia' (FRDC Project 98/108). A closely related project proposal is the 'Northern Australian sharks and rays: the sustainability of target and bycatch species, Phase 2' (FRDC Project 2002/064). Data from the present project proposal fed directly into the 'Ecological Risk Assessment for Australian Commonwealth Fisheries Project' (AFMA Project R01/0934 and AFMA Project R04/1072).

Similarly, species investigated through projects off Western Australia—notably whiskery shark (*Furgaleus macki*) and dusky shark (*Carcharhinus obscurus*)—did not need be examined by the present project. The projects include 'Stock assessment of large coastal and demersal species' (FRDC Project 93/067) and 'Biology and stock assessment of Western Australia's commercially important shark species' (FRDC Project 1996/130). Pelagic sharks (notably blue shark, mako, and thresher sharks) will not be included; these species have been investigated by CSIRO through 'A review of Australia's pelagic shark resources' (FRDC Project 98/107) and by various overseas studies. An east coast related project is 'Data analysis of NSW fishery-independent surveys on SEF trawl grounds' (FRDC Project 96/139).

Need

The Environment Protection and Biodiversity (EPBC) Act 1999 imposed new assessment requirements for Commonwealth managed fisheries and all fisheries exporting product. Management plans and policies now have to be strategically assessed by the Australian Minister for the Environment and Water Resources before they are finalised. The requirements apply to all Commonwealth managed fisheries that did not have an approved statutory management plan when the Act came into force on 16 July 2000. The requirements for assessment are set out in EPBC Act 1999 and the Minister for the Environment and Water Resources advised AFMA that strategic assessment reports must, as part of their terms of reference, address the ecological sustainability guidelines, which were initially prepared for Schedule 4 of the Wildlife Protection Regulation of Exports and Imports Act 1982 (WP(REI) Act). This process involves *inter alia* assessing each fishery for ecological impacts on (a) target and by-product species, (b) bycatch species, (c) threatened, endangered, and protected species, (d) marine habitats, and (e) marine food chains. For each of these items of ecological impact, there has to be available data, risk assessments, and management responses. To assist AFMA in drafting the strategic assessment report and to highlight the requirements of strategic assessments to stakeholders, AFMA held several workshops for the GHATF, SETF, and GABTF during mid-2001.

In addition, through the former Standing Committee on Fisheries and Aquaculture, all Australian Commonwealth and State fisheries ministers endorsed the National Policy on Fisheries Bycatch, which includes sharks and other chondrichthyans. Consistent with Commonwealth policy and legislative obligations under Australia’s Ocean Policy regarding the impact of fishing activities on non-target species and the environment, AFMA has Bycatch Action Plans for major Commonwealth fisheries. The Bycatch Action Plans demonstrate a commitment to minimise bycatch and address the requirement under the Australian Fisheries Management Act 1991. The requirement under the Act is to “ensure that the exploitation of fisheries resources and the carrying on of 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”.

To meet all these requirements, there was an urgent need to develop a staged set of methods, which can be applied across species, biotic communities, and ecosystems to all Commonwealth fisheries to enable a coordinated and comprehensive assessment strategy. Such an approach must be scientifically defensible, but also pragmatic (applicable across a wide range of situations including type of fishery and varying availability of data). AFMA funded a project titled ‘Ecological Risk Assessment for Australian Commonwealth Fisheries’ to develop hierarchically appropriate methods and to begin undertaking ecological risk assessments. This was a broad ranging project involving widespread collaboration between researchers at CSIRO Marine and Atmospheric Research (Hobart and Cleveland centres), AFMA, BRS, and MAFFRI.

The ERA Project began during October 2001 and resolved methods to be applied in the hierarchical risk framework. The project reviewed existing risk assessment methods and approaches, and extended methods, and advised on appropriate approaches to each Commonwealth fishery. The project evaluated data available, data from other current projects, and identified the additional data sets required for ecological risk assessment. For SESSF, it was recognised that SharkRAG, SEFRAG, and GABRAG needed to initiate projects for the collection of appropriate data for undertaking ecological risk assessment. Chondrichthyans were identified as a group where many of the species have low ‘biological productivity’ and therefore potentially at high ecological risk in several Commonwealth fisheries.

There are several reasons why chondrichthyans need special attention and why the present FRDC project focused only on this group of fishes.

1. The life-history characteristics of chondrichthyan species make for low ‘biological productivity’ and cause these animals to be generally more vulnerable to the effects of fishing than teleost and invertebrate species. The comparatively low ‘biological productivity’ of chondrichthyans has raised considerable national and international concern over their population status.
2. Assessment methods applicable to chondrichthyan species differ from those applicable to teleosts and invertebrates.
3. Most of the previous research effort on chondrichthyan species in southern Australia has been directed at target species (gummy shark) and major byproduct species (school shark, common sawshark, southern sawshark, and elephant fish), whereas minor byproduct and bycatch species have received little or no attention.
4. Unlike the more highly productive teleost and invertebrate species, which can have highly variable population sizes from year to year, the comparatively low ‘biological productivity’ of chondrichthyan species provides for very stable populations. These species are therefore ideal for monitoring the long-term trends in the ecosystem, particularly the highly abundant species such as the draughtboard shark, Port Jackson shark, and piked dogfish, which are bycatch species mostly discarded live.

Worldwide concern for the condition of the stocks of chondrichthyan species led to development of the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks), by the Food and Agriculture Organisation of the United Nations (FAO), where the term 'shark' is taken to include shark, ray, and holocephalan species. The IPOA-Sharks was ratified by the FAO Committee of Fisheries during February 1999 and now recognises that these species require special management, research, and monitoring if they are to be harvested sustainably (Anon. 2000).

Australia, as a signatory to the IPOA-Sharks, was obliged to prepare a Shark Assessment Report and to develop a Shark Plan as part of its National Plan of Action for the Conservation and Management of Shark (NPOA-Sharks). Preparation of Australia's Shark Assessment Report and Shark Plan was undertaken by the Shark Advisory Group (SAG), which was established by DAFF with membership from DEWR, AFMA, the states, selected industry personnel, and shark specialist researchers. Progress on development of Australia's Shark Assessment Report and Shark Plan was first reported to the FAO Committee of Fisheries during February 2001 and launched during May 2004. The Shark Implementation and Review Committee (SIRC) is monitoring progress on implementation of Australia's Shark Plan.

The Shark Assessment Group and the current Australian NPOA-Sharks identified risk assessment of Australian chondrichthyans, undertaken with a national approach, as high priority research. Risk assessment is fundamental to the NPOA-Shark and management agencies' ability to prioritise their actions for the conservation and management of sharks, rays, and holocephalans. The risk assessment undertaken in the present project contributes directly to this. To achieve a national approach, the present project is aligned strongly with FRDC Project 'Northern Australian sharks and rays: the sustainability of target and bycatch fisheries, Phase2' (FRDC 2002/064). Together the two projects will produce compatible risk assessments of chondrichthyans in line with the recommendations of the NPOA-Shark.

Concurrently, the International Union of Conservation Nations (IUCN) Shark Specialist Group categorised the chondrichthyan species it has considered world-wide as follows: critically endangered (8 species), endangered (16), vulnerable (20), lower risk (near threatened) (31), lower risk (conservation dependent) (8), data deficient (14), and lower risk (least concern) (5).

In southern Australia, several species of shark have been identified as requiring special protection or management. The white shark (*Carcharodon carcharias*) is listed as 'vulnerable' and the grey nurse shark (*Carcharias taurus*) is listed as 'critically endangered' for east coast population and 'vulnerable' for the west coast population under the EPBC Act 1999. The Commonwealth and various States have special protection for the basking shark (*Cetorhinus maximus*). On the continental slope, several species of dogfishes (Squaliformes) and holocephalans (Holocephaliformes), taken as byproduct and bycatch, are severely depleted and require special management. Species such as *Centrophorus harrissoni*, *C. zeehani* (syn. *C. uyato*), and *C. moluccensis* have been considered for listing under the EPBC Act 1999, but are now given some protection by several closed areas.

Objectives

1. Quantitatively categorise bycatch species of shark and other chondrichthyans taken in the GHATF, SETF, and GABTF based on 'relative biological productivity'.
2. Semi-quantitatively categorise chondrichthyan bycatch species taken in these fisheries based on 'catch susceptibility' determined from availability, encounterability, selectivity, and post-capture mortality to the fishery based on presently available data.
3. Semi-quantitatively determine diets of chondrichthyan bycatch species taken in these fisheries from analysis of stomach contents analyses to contribute to establishing their positions in marine food chains.
4. Resolve taxonomic uncertainties of various chondrichthyan species, particularly uncertainties among dogfish species.
5. Undertake assessment of sustainability for ecological risk for each chondrichthyan bycatch species through the application of rapid assessment techniques developed through the AFMA funded project

titled 'Ecological Risk Assessment for Australian Commonwealth Fisheries'.

6. Address the sustainability and ecological risk of endeavour dogfish, Harrison's dogfish, southern dogfish and other dogfish species with high priority.

Methods

Determination of species lists

Catch evaluation and trend analysis were incorporated into the rapid assessment of ecological risk from the effects of fishing using the results from FRDC Project 2000/007 (Walker and Gason 2007). Those results indicate the number of separate species identified by the ISMP, which used together with the scientific literature indicate the species that occur predominantly within the range of the SESSF. Estimates of mean annual catch during 2000–06, based on data from the ISMP, provided a basis for arbitrarily classing species as 'rare' where mean annual catch is <1 t, 'sparse' where catch is 1–19 t, 'common' where catch is 20–99 t, and abundant where catch is ≥100 t.

Catch evaluation and trend analysis

The mean annual total-catch mass for each species during 2000–06, within each fishery sector of the SESSF, was estimated in two steps. The first step was to estimate mean CPUE for total catch mass for each sector from ISMP data. The second step was to weight the mean CPUE for each species within each sector by the mean annual number of shots of the gear reported on fisher logbooks to determine total catch. The estimates of mean annual catch of each species was determined as the sum of the estimated catches for GABTF otter trawl, SETF otter trawl, SETF Danish seine, GHATF trap, GHATF dropline, GHATF automatic longline, GHATF scalefish longline, and GHATF scalefish gillnet. These catch masses were determined separately within each of three bathometric depth-ranges (0–199 m, 200–599 m, and ≥600 m) and for all depths combined during 2000–05 (Walker and Gason 2007).

Trend analysis was based on ISMP data from the GABTF and SETF. The ISMP monitors the GABTF from Cape Leeuwin (34° 22′ South, 115° 08′ East) in Western Australia to Cape Jervis (35° 37′ South, 138° 05′ East) in South Australia. The ISMP also monitors the SETF from Cape Jervis in South Australia to Barranjoey Head (33° 35′ South, 151° 20′ East) in New South Wales. The data are distinguished between the two fishery sectors by the meridian of longitude 138° East. Data are available since 2000 from the GABTF and since 1992 from the SETF. Because of large differences in the periods of the time series of data and limited overlap in the vessels between the GABTF and SETF, data from the two fishery sectors were mostly analysed separately, but were combined for some species.

Standardisation of CPUE involved an initial "data selection process" to exclude regions and depths where a species had not been detected and then analysed using the GENMOD procedure of the statistical package SAS/STAT. The GENMOD procedure fits generalised linear models (Nelder and Wedderburn 1972) to data by maximum likelihood estimation of parameters through an iterative fitting process. The GENMOD Type 3 Analysis was adopted because design of the data is non-orthogonal and because the results do not depend on the order in which the explanatory variable terms in the model were fitted to the data. For depicting temporal and spatial trends in relative abundance, the explanatory variables included year, month, locality, bathometric depth-interval, and vessel, where locality is treated as a one degree longitude-interval or a one degree latitude-interval ('long-lat'). To address statistical complexities associated with large proportions of zero catch rates for many species the delta-x model formulation was adopted where non-zero CPUE values were modelled with log-gamma pdf combined with the binomial pdf where CPUE=0 was assigned a value of 0 and CPUE>0 a value of 1. Standardised CPUE in locality-cells (one degree of latitude or one degree of longitude by depth-interval) were weighted by the "habitat area" in each cell (Walker and Gason 2007).

Collection and laboratory preparation of specimens

Collection of specimens for dissection involved fishers collecting, holding, and dispatching animals to the laboratories of MAFFRI in Queenscliff, Victoria, and of CSIRO Marine and Atmospheric Research in Hobart.

In some cases, specimens were provided by onboard scientific observers associated with the Integrated Scientific Monitoring Program (ISMP). For some species, fishers were accompanied at sea to collect specimens.

There were five impediments to the collection and laboratory processing of species required for a comprehensive study of this type. The first impediment was the high cost of large specimens of target and byproduct species, such as broadnose sevengill shark (*Notorynchus cepedianus*) and angel sharks (*Squatina* spp) that are normally marketed. The second impediment was the large size of specimens of many chondrichthyan species. It was unreasonable to expect fishers to handle manually large animals that are normally discarded, which in certain cases weigh >100 kg and take up excessive space in their freezers or brine tanks, e.g. common stingray (*Dasyatis brevicaudata*) and black stingray (*D. thetidis*). This incurred costs associated with chilling, handling, and transporting of specimens. The third impediment was the difficulty collecting the full size range of male and female specimens and collecting animals in all of the various reproductive conditions; e.g. shark gillnets retain small immature sevengill sharks, but not large mature animals. The fourth impediment was difficulty ageing many species. This required special developmental work for deep-water dogfish (family Squalidae) (Irvine 2006), Port Jackson shark (*Heterodontus portusjacksoni*) (Tovar-Ávila *et al.* in press), whitefin swell sharks (Bell in preparation), and holocephalans (Bell in preparation). Attempts made to develop methods for ageing angel sharks, sevengill sharks, and several species of catshark have so far been unsuccessful. The fifth impediment was the rarity of a large proportion of the chondrichthyan species caught in the SESSF. For example, of 137 species of chondrichthyan species recorded in the catch from the SESSF as part of the ISMP, <1 tonne was caught for each of 55 species, and 1−19 tonne for a further 43 species; it was particularly difficult to obtain adequate sample sizes for many of these 98 species (Walker and Gason 2007). For several species, particularly widely distributed pelagic sharks, it was possible to use published results.

The methods are described briefly under the following six separate headings, one to address each of the six project objectives. Further details of the methods are contained in the various manuscripts presented as appendices to the main report.

Biological productivity

Populations of shark and other chondrichthyan species tend to have lower reproductive rates and lower natural-mortality rates than populations of teleost and invertebrate species. Chondrichthyan animals can be characterised as having late maturity, low fecundity, and parturition cycles often exceeding one year that provide for a close stock-recruitment relationship. Low but relatively constant reproductive rate and low natural mortality rate provide for relatively little inter-annual variability in response to environmental variation and for long stock-recovery periods in response to overfishing. Consequently, for many chondrichthyan species, only a relatively small proportion of the population can be removed annually if the catches and populations are to remain sustainable. Such populations have low biological productivity. Species with high biological productivity have high reproductive rates and high natural mortality rates, and a high proportion of the biomass can be harvested from the population sustainably.

Species of high ‘biological productivity’ can be viewed as having rapid population turnover, whereas species of low biological productivity can be viewed as having slow population turnover. For an unexploited population to remain in equilibrium there has to be a balance between the natural mortality rate reducing numbers and the reproductive rate increasing numbers. Otherwise, over time, if the reproductive rate exceeded the natural mortality rate, the population would grow to infinity, and, conversely, if the natural mortality rate exceeded the reproductive rate, the population would go extinct.

Low reproductive rate and low natural mortality rate are associated with low biological productivity, whereas high reproductive rate and high natural mortality rate are associated with high biological productivity. It follows, therefore, that either reproductive rate or natural mortality rate can serve as a proxy for biological productivity for rapid assessment (Walker 2005a).

Other expressions of biological productivity include the ‘intrinsic rate of population growth’ parameter formulated variously in biomass dynamics models (Schnute 1985; Schnute 1987), demographic models (Lotka 1922), and various adaptations of these models for sharks (Au and Smith 1997). Using a particular formulation of a demographic model to allow for density-dependent change in natural mortality (Au and Smith 1997), one study classed 26 Pacific shark species on the basis of the ‘intrinsic rate of population growth' (referred to by the authors as 'rebound potential') (Smith *et al.* 1998). In addition, 'intrinsic rate of population growth' is related to inter-generation period and reproductive output per generation. Application of biomass dynamics models requires time series of catch and relative abundance data, and demographic analysis combines available parameter estimates for natural mortality rate and reproduction.

Required information for this purpose on chondrichthyan reproduction for a population includes the maternity ogive (proportion of the female population contributing to annual recruitment expressed as a function of length or age), fecundity expressed as a function of maternal length or age, and sex ratio of progeny. Where parturition is annual, the maturity ogive approximates to the maternity ogive. If the maternity ogive and fecundity are expressed as a function of length, then the relationship between length and age is also required for the application of demographic models. There are also advantages in having various morphometric and isometric relationships to aid fisheries management.

Hence, for the present study, where there were sufficient data, parameters estimates were determined for natural mortality from data on maximum age and for the following relationships:

1. body mass–length and other morphometric relationships,
2. frequency of parturition from timing of ovulation and parturition and from period of gestation,
3. maturity–length and maternity–length relationships,
4. litter size–maternal length relationship, and
5. von Bertalanffy length–age relationships.

Natural mortality

Using natural mortality rate, M, as a proxy for biological productivity requires some caution, as the natural mortality rate is likely to be density-dependent and age-dependent. Also, fishing is likely to remove the oldest animals from the population and reduce the maximum age detected in a sample of animals collected for ageing purposes. Notwithstanding these potential biases, rough estimates of natural mortality or maximum age can be used for broad categorisation of risk. The instantaneous total mortality rate (natural mortality and fishing mortality rates combined), Z, can be approximately related to maximum age, t_{max}, by the equation $\ln(0.01) = -Z\ t_{max}$ where 0.01 represents survival of 1% of the animals reaching maximum age (Hoenig 1983). Because natural mortality rate is much higher for the young age-classes than the older age-classes, as demonstrated from modelling shark populations (Punt and Walker 1998; Walker 1992), this equation is reformulated here for application to chondrichthyan populations by considering only that part of the population of age greater than 2 years. Assuming that mortality is constant for all age-classes greater than 2 years, calculations of instantaneous total mortality rate for 1% of 2-year-old animals to survive to ages 8, 16 and 24 years are 0.77, 0.33 and 0.21, respectively. If total mortality is divided evenly between natural mortality and fishing mortality (i.e. Z=2M), a condition sometimes assumed for a population in equilibrium producing approximately the maximum sustainable yield (Thompson 1992), natural mortality rates for 2-year-old animals surviving to these ages approximate to 0.38, 0.16 and 0.10, respectively. These values are used as a basis for arbitrary categorisation of chondrichthyan species for risk. In southern Australia on the continental slope, it is likely that Z>2M for many of the chondrichthyan species. For example, based on published instantaneous natural mortality rates, *Galeorhinus galeus* (Punt and Walker 1998; Smith *et al.* 1998), *Carcharodon carcharias*, C*archarias taurus*, *Carcharhinus plumbeus* and *C. obscurus* (Smith *et al.* 1998) can be classed as having low natural mortality and hence at high risk from effects of fishing. Similarly, *Mustelus antarcticus* (Walker 1992), *M. californicus*, *M. henlei* and *Sphyrna tiburo* (Smith *et al.* 1998) can be classed as having medium natural mortality and hence at medium risk, and *Rhizoprionodon terraenovae* can be classed as having high natural mortality and hence at low risk (Smith *et al.* 1998).

Age and growth

Several alternative methods were adopted for ageing chondrichthyan species because of differences in the readability of growth-increment banding in hard tissue parts (vertebrae or dorsal fin-spines) between different species. Although all species have vertebrae, the vertebrae do not calcify with visible bands in sixgill and sevengill sharks (order Hexanchiformes) or holocephalans (Holocephaliformes) and, in angel sharks (Squatiniformes), the vertebrae calcify, but do not have annual banding and, therefore, cannot be aged from vertebrae. Only three chondrichthyan groups—dogfishes (Squaliformes), horn sharks

(Heterodontiformes), and holocephalans (Holocephaliformes)—possess dorsal fin-spines. Unless ageing methods based on other hard-tissue types are developed, the dorsal fin-spines provide the only available hard tissues that can be used for ageing species of Holocephaliformes and are favoured over vertebrae for ageing species of Squaliformes and Heterodontiformes. Catsharks and carpet sharks (Orectolobiformes) were difficult to age using standard methods.

As part of the present study, it was necessary to develop new methods of ageing for some chondrichthyan groups. New methods were developed for ageing species of horn sharks as applied to the Port Jackson shark (*Heterodontus portusjacksoni*) (Tovar-Ávila *et al.* in press), holocephalans (Bell in preparation), catsharks as applied to the whitefin swellshark (*Cephaloscyllium* sp A) (Bell in preparation), and dogfishes (Irvine 2006). Ageing chondrichthyan animals involves the choice of reading external growth-increment bands on the surface of vertebrae or dorsal fin-spines or reading internal growth-increment bands in sections of vertebra centra or dorsal fin-spines. Full analysis comparing the differences in age estimates provided by the different methods, as undertaken for gummy shark (*Mustelus antarcticus*) and school shark (*Galeorhinus galeus*) as part of FRDC Project 1991/037 (Officer *et al.* 1996), were beyond the scope and resources of the present study. Similarly, validation of the method of ageing these species by oxytetracycline injection of tagged sharks in the wild, as undertaken for *M. antarcticus* and *G. galeus* as part of FRDC Project 1997/110, were beyond the scope and resources of the present project (Walker *et al.* 2001).

Ages were estimated by assuming counted growth-increment bands are deposited annually. For species where sample size was adequate, the length-at-age data were fitted to the von Bertalanffy growth model. The growth model has the equation

$$l_a = L_\infty\{1 - e^{-K(a-a_0)}\}$$

where K, L_∞ and a_0 are the growth parameters and l_a is the length of a shark at age a. The parameter estimates and maximum age estimates are presented as results. Results from earlier studies are presented where adequate data were available.

Reproductive biology

Data management and statistical analysis procedures developed as part of the present project enabled rapid processing and analysis of the data to provide the required outputs. Nevertheless, as the data for each species were analysed, the analysis procedures improved and often provided insights that could be applied to other species. One of the complexities of this work is that the mode of reproduction varies between the species of sharks, rays, and holocephalans. Some species are oviparous (egg laying), whereas others exhibit aplacental viviparity (viviparous without a placenta), or placental viviparity (viviparous with a placenta). Ovulation and parturition (birth) are synchronous for some species (Walker 2007), but asynchronous for others (Braccini *et al.* 2006). In addition, parturition can vary as annual, biennial, triennial, or longer. Hence, different approaches to data analysis had to be taken depending on the mode of reproduction and peculiarities of the species.

In addition, simple demographic models are applied to provide estimates of mortality rate and reproductive rate to serve as proxies for classing biological productivity as high, medium, and low. For some species, notably cosmopolitan pelagic species, it was possible to use published information.

A full description of the methods adopted for determining the reproductive parameters required for rapid assessment or fishery stock assessment are described in detail in each of several quantitative reproductive papers either published (Appendix 7), in press (Appendix 8), or in preparation (Appendix 9). A more general paper published as part of FRDC Project 1999/103 develops methods for application to chondrichthyans in general, which is applied to school shark (Walker 2005b). The peculiarities of the structure and function of various reproductive organs and tissues of chondrichthyans were investigated and published in scientific journals (Hamlett *et al.* 2002; Reardon *et al.* 2002; Smith *et al.* 2004), book chapters (Hamlett *et al.* 2005; Jones *et al.* 2005), and a thesis (Storrie 2004) as part of FRDC Project 1999/103 or the present project.

The total body mass, w, to total length (TL), l, relationship was determined using the power curve

$$w = acl^b ,$$

where a and b are parameters determined by linear regression of the natural logarithm of w against the natural logarithm of l, and c is a factor correcting for bias caused by natural logarithmic transformation (Beauchamp and Olson 1973; Walker 2007).

The relationship between the number of macroscopically visible embryos *in utero*, p, and maternal TL, l is represented by the linear equation (Walker 2005b) given by

$$p = a + bl,$$

or by the power equation (Mollet *et al.* 2000) given by

$$p = al^{b},$$

or by the exponential equation (Walker 2007) given by

$$p = ce^{a+bl},$$

where a and b are parameters estimated by linear regression, and c is a coefficient for correcting bias caused by logarithmic transformation of p for the regression (Beauchamp and Olson 1973). Where there are insufficient data to determine the appropriate relationship, p is represented by the macroscopically visible number of embryos *in utero*.

The period of gestation and growth of embryos were determined by plotting mean TL of embryos observed in pregnant females with *in utero* embryos and mean TL values of 0 for *in utero* eggs observed in pregnant females against month and then evaluating the seasonal pattern.

The ovarian cycle was investigated by examining the ovary and measuring the diameters of the largest follicles in animals caught throughout the year. The largest follicle diameter (LFD) varied widely between individual animals and varied depending on uterus condition, so seasonal pattern in LFD for each of the six uterus conditions was examined separately. Pregnant females with macroscopically visible *in utero* embryos provided the least ambiguous basis for determining seasonal growth rates of follicles. Annual growth rate of follicles for pregnant females with macroscopically visible embryos was determined by the linear relationship between LFD, o, and day of year, t, given by

$$o = a + bt,$$

where a and b are parameters estimated by linear regression. Scattergrams of LFD against day of year for each uterus condition were compared with the regression line and its and 95% prediction intervals used as a basis for distinguishing between annual, biennial, and longer ovarian cycles (Walker 2007).

Size-at-maturity and size-at-maternity were determined as the proportion of the population of animals mature at any TL by classing each animal as in mature condition or immature condition and applying logistic regression for females and males separately. Similarly, for females, the proportion of the population of animals in maternal condition at any TL can be determined by classing each animal as in maternal condition or non-maternal condition and applying logistic regression. A female was classed as in mature condition if the largest ovarian follicle was >3 mm in diameter (approximate size when vitellogenesis begins following folliculogenesis); otherwise it was classed as in immature condition. Given uncertainty of the best indicator of maturity of males, the results from methods based on alternative criteria for assuming the mature condition and the immature condition were compared. Males were classed as mature or immature based on testis development, seminal vesicle condition, or clasper calcification. A female was classed in maternal condition at the time of capture, if, had it survived, it would have given birth to young before or soon after a particular date (e.g. 1 January for *Mustelus antarcticus*) (Walker 2007); all other females were classed in non-maternal condition.

Logistic regression was adopted to determine the proportion of females in mature condition, the proportion of males in mature condition, and the proportion of females in maternal condition as a function of TL. Females or males in mature condition were assigned a maturity condition value of 1, whereas those in immature condition were assigned a maturity condition value of 0. Similarly, females in maternal condition were assigned a maternal condition value of 1, whereas females in non-maternal condition were assigned a maternal condition value of 0.

The logistic equation adopted to express P as a function of l is given by

$$P = P_{\max}\left(1+e^{-\ln(19)\left(\frac{l-l_{50}}{l_{95}-l_{50}}\right)}\right)^{-1},$$

where $P_{\max}$ is the maximum proportion of animals in mature condition or maternal condition, and l_{50} and l_{95} are the lengths at which 50% and 95% of the maximum proportion of animals in mature condition or maternal condition (Walker 2005b; Walker 2007). The parameters $P_{\max}$, l_{50} and l_{95}, with 95% confidence intervals, were estimated by the method of maximum likelihood using the probit procedure (Proc Probit) of the computer statistical package SAS (SAS Institute, Cary, North Carolina, USA). This applies a modified Newton–Raphson algorithm for estimation. $P_{\max}$ normally has a value of 1.00, except when parturition frequency is biennial ($P_{\max} = 0.500$) (Walker 2007), triennial, ($P_{\max} = 0.333$) or some other period (Walker 2005b).

Unlike maximum, which can give a direct measure of biological productivity, combining the maternity or maturity ogive with the relationship of between the number of embryos and maternal length requires models and assumptions. To provide the simplest metric from combining these relationships , where the appropriate parameters are available, values of the mean number of embryos or eggs produced annually at length, l_{50}, are presented for comparison purposes.

Catch susceptibility

‘Catch susceptibility’ has four parts 'availability', 'selectivity', 'encounterability', and 'post-capture mortality'. The method is applied to each of the five major fishing methods in the Southern and Eastern Scalefish and Shark Fishery (SESSF): demersal trawl, shark gillnet, shark longline, automatic longline, and trap. An estimate of ‘catch susceptibility’ is provided for each SESSF method for each chondrichthyan species occurring in south-eastern Australia in the attached table. Also included is information on distribution and relative abundance.

In fishery models, fishing mortality rate for a harvested population is usually expressed as the product of the two quantities ‘fishing effort’ and ‘catchability’. Fishing effort can be quantified as the number of fishing vessels in a fleet, or a measure of the amount of fishing gear deployed, amount of fishing time, or some other variable that is a mix of these variables. ‘Catchability’ is the proportion of the exploited population taken by one unit of fishing effort and has a value in the range 0–1 for any age or size of fish. It is the product of three parameters, each of which also has a value 0–1. The three parameters comprising catchability are ‘availability’, ‘encounterability’, and ‘selectivity’; i.e.

catchability = availability x encounterability x selectivity.

Availability’ is the proportion of the habitat area of a population fished by the fleet. A population with a habitat area extending well beyond the range of the fishing fleet has a low availability value. Conversely, a population with a habitat area that falls entirely inside the range of the fishery has a high availability value of 1, unless parts of the habitat area are inaccessible to the fishing fleet.

‘Encounterability’ is the proportion of that part of the population available to fishery encountered by one unit of fishing effort. For any species, encounterability depends on construction the fishing gear and on the biological characteristics of that species. Pelagic and semipelagic species that actively swim in the water column are more likely than less active species to encounter passive gears such as gillnets or longlines with baited hooks. These actively swimming species therefore have a higher encounterability to these gears than the less active species. For active gears such as demersal trawl, bottom-dwelling, sluggish species, such as the angel shark (*Squatiniformes*) and batoids have a higher probability of capture and therefore higher encounterability than the more powerful swimming species, such as the whaler (*Carcharhiniformes*) and mackerel (*Lamniformes*) sharks. Sixgill and sevengill sharks (*Hexanchiformes*), sawshark (*Pristiophoriformes*), dogfishes (*Squaliformes*), catsharks and wobbegong and carpet sharks (*Orectolobiformes*), and horn sharks

(*Heterodontiformes*) probably exhibit intermediate trawl encounterability (Walker 2005a).

'Selectivity' is the proportion of the animals encountering the fishing gear that is captured. For any fishing gear, selectivity gives rise to a range of complex dynamics that relate features of the fishing gear to size of animals captured. Selectivity by trawl nets for size of chondrichthyan animals is not well understood, and hook-size selectivity for size of animal is weak. For gillnets, however, sharks and other chondrichthyan fish of different sizes are not equally vulnerable to capture. Small animals swim through gillnets but become progressively more vulnerable to capture as they grow. After reaching the length of maximum vulnerability they then become progressively less vulnerable with further growth as they deflect from the meshes of the nets (Kirkwood and Walker 1986). These size selectivity effects are stronger for fusiform-shaped sharks than for more dorsoventrally-flattened species or for species with protruding structures such the heads of hammerhead sharks, the rostral teeth of pristiophorid sawsharks and pristid sawfishes, and the dorsal fin-spines of squalid and heterodontid sharks and chimaerids. When captured by gillnet or hook, fast swimming species, dependent on ram-jet ventilation of their gills for respiration tend to die more quickly than bottom-dwelling species when caught. Bottom-dwelling species with spiracles to aid gill ventilation are better able to pass water over their gills after capture by gillnets and can struggle vigorously to either escape or become more tightly enmeshed in the gear. Species that can struggle more vigorously after capture in gillnets tend to have narrower selectivity ranges than species that cannot struggle. Hence, for some species, careful regulation of mesh-size can be used to ensure that the sharks captured are large enough to avoid growth overfishing and small enough to facilitate escapement of large breeding animals to avoid recruitment overfishing (Walker 1998). For the purpose of the present study, relative selectivity is assumed for to be constant over all size of chondrichthyan animals for hooks and trawl, but dome-shaped for gillnets of 6–6½-inch mesh-size adopted in the GHATF. The method developed by Kirkwood and Walker (1986) was applied to available gillnet selectivity parameters for gummy shark (*Mustelus antarcticus*) (Kirkwood and Walker 1986), school shark (*Galeorhinus galeus*), common sawshark (*Pristiophorus cirratus*), southern sawshark (*Pristiophorus nudipinnis*) and elephant fish (*Callorhinchus milii*) determined as part of FRDC Project 1999/103 (Walker and Hudson 2005b). For all other byproduct or bycatch species taken by shark gillnets in the GHATF, relative selectivity was calculated by dividing the catch rate data for 6-inch mesh-size by the highest catch rate for any mesh-size in the range 2–9-inch mesh size using data from gillnet selectivity experiments undertaken during 1973–76 and collated as part of FRDC Project 1999/103 (Walker *et al.* 2005b).

The concept of catchability is usually applied to target and byproduct species where most of the animals captured are retained. So as to broaden the concept to include bycatch, the term 'catch susceptibility' (Stobutzki *et al.* 2001; Stobutzki *et al.* 2002) and the term 'post-capture mortality' are adopted here to allow for survival of part of the catch released. The parameters 'catch susceptibility' and 'post-capture mortality' both have values in the range 0–1 and are related to each other and to catchability by the equation

$$\text{catch susceptibility} = \text{catchability} \times \text{post-capture mortality},$$

which can hence be further expanded to provide the equation

$$\text{catch susceptibility} = \text{availability} \times \text{encounterability} \times \text{selectivity} \times \text{post-capture mortality}.$$

'Post-capture mortality' is the proportion of the animals that die as a result of being caught in the fishing gear. Animals of target and byproduct species that are mostly retained have a post-capture mortality value approaching 1. This can be less if some are discarded because of their size or breeding condition. Post-capture mortality for discarded species can vary markedly. In addition to handling by fishers, the fishing gear and biological characteristics can contribute to various kinds of mortality referred to as 'unaccounted fishing mortality' or as 'collateral mortality'. Dead sharks not tightly enmeshed can drop out of gillnets and contribute to 'unaccounted fishing mortality' through 'drop-out mortality'. Sharks eaten by other fish or mammals after capture in the gear contribute to 'unaccounted fishing mortality' through 'predation mortality'. Dead sharks either partly or totally decomposed or eaten by invertebrates and vertebrates when fishing gear is left in the water for extended periods also contributes to 'unaccounted fishing mortality'. Also, lost gillnets contribute to 'unaccounted fishing mortality' through 'ghost fishing mortality' until they are rolled into a ball by tidal flow. Post-capture mortality from normal handling by fishers is low for heterodontid and orectolobid sharks but high for carcharhinid sharks.

Catch susceptibility and each of its four parts are arbitrarily divided into three categories of risk. This is achieved here by evenly dividing the possible value range of 0.00–1.00 into the three ranges 0.00–0.33, 0.34–

0.66 and 0.67–1.00 and designated low (L), medium (M) and high (H), respectively. For each of the five major fishing methods in the SESSF, each of 'availability', 'encounterability', 'selectivity' and 'post-capture mortality' are classed as low, medium or high for each chondrichthyan species. By adopting the upper limit values for the three ranges of 0.33, 0.66 and 1.00 for low, medium and high risk, respectively, then catch susceptibility can also be categorised as low, medium or high risk. For example for a fishing method where availability is low, encounterability is high, selectivity is high, and post-capture mortality is high, then 'catch susceptibility' is low. This is calculated as 'catch susceptibility' = 0.33 x 1.00 x 1.00 x 1.00 = 0.33 (i.e. 'catch susceptibility' = LHHH = L) (Walker 2005a).

Trophic position

Stomach contents analyses were used for classing each chondrichthyan species to a trophic position based on relative mixes of diets of nekton, pelagic prey (squid, clupeoids, mackerel), demersal fish, epibenthic invertebrates (crustaceans, molluscs, echinoderms, octopus, cuttlefish, polychaetes, and sipunculids), and mammals (seals and dolphins). This is assessed for each chondrichthyan species, where feasible, by determining 'frequency of occurrence', 'prey mass' (or 'prey volume') and 'prey number' for each species of prey item. In addition to determining trophic level, these data will be valuable in for ecosystem modelling and can be used for classing each chondrichthyan species as, firstly, an 'obligate' or 'generalised' feeder, and, secondly, as a pelagic, bentho-pelagic, or demersal feeder.

An index of standardized diet composition was calculated for each species as a weighted average that can incorporate data from multiple quantitative dietary studies and can account for sample size (number of stomachs examined) in each study. The equation to calculate the proportion of each prey category, P_j, in the diet is

$$P_j = \frac{\sum_{i=1}^{n} P_{ij} N_i}{\sum_{j=1}^{11} (\sum_{i=1}^{n} P_{ij} N_i)},$$

where P_{ij} is the proportion of prey category j in study i, N_i is the number of stomachs with food used to calculate P_{ij} in study i, n is the number of studies, j is the number of prey categories (11), and P_j=1. For each study, P_{ij} values were calculated using the quantitative method used in the original study, with the following ranking criteria aimed at characterizing the diet more accurately based on percent weight (%W) or percent volume (%V) (Cortés 1999).

Trophic levels (T_k) were then calculated for each species (k) as

$$T_k = 1 + \sum_{j=1}^{11} P_j T_j$$

the trophic level of each prey category j. Trophic level (T) of the 11 prey categories was taken from a published account (Cortés 1999). These published values were taken from published values derived through ecosystem modelling. The 11 prey categories used to calculate standardized diet compositions and trophic level of each chondrichthyan species are listed as follows.

Code	Species group	Trophic level
Mammal	Marine mammals	4.02
Bird	Seabirds	3.87
Chondrichthyes	Chondrichthyan fishes	3.65
Teleost	Teleost fishes	3.24
Cephapopoda	Cephalopods	3.20
Crustacea	Decapod crustaceans	2.52

Invertebrates	Other invertebrates, except molluscs, crustaceans, & zooplankton	2.50
Marine reptiles	Marine reptiles (sea turtles and sea snakes)	2.40
Zooplankton	Zooplankton (mainly krill)	2.20
Mollusc	Molluscs, except cephalopods	2.10
Plants	Plants (marine plants and algae)	1.00

Marine food webs in which chondrichthyan species occur have more than four trophic levels where chondrichthyans occupy the upper trophic positions. Although long food chains can provide for dynamic stability (Sterner *et al.* 1997), high trophic species such as the chondrichthyans have top-down effects because upper level species are dependent on prey species at lower levels. Bottom-up effects of lower trophic level organisms through mass transfer ultimately reaching chondrichthyan species are not so well understood. At the ecosystem level, removal of portions of the biomass of one or more species from the effects of fishing results in adjustments to the dynamics and community composition of an otherwise stable ecosystem; however, excessive removal can lead to a trophic cascade (Daskalov 2002; Francis *et al.* 2007). At the individual species level, on the other hand, the stability of a particular species is not only directly affected by removal of biomass of that species, but also those species at a lower trophic level on which it preys. Hence, for ecological risk assessment, species at the high the trophic levels are at greater ecological risk than those at lower trophic levels. For the present study, a trophic level above 4.25 is classed as high risk, 4.00–4.25 is classed as medium risk, and below 4.00 is classed as low risk.

Resolving taxonomic uncertainty

There have been a number of taxonomic problems within several genera in Australia, which have important implications for their conservation status and management. These genera have mostly been reported to have widespread distributions. However, several of the nominal species actually appear to be complexes of closely related species.

Various morphological, morphometric and meristic methods were applied to resolve taxonomic uncertainties associated with the genera of *Orectolobus* (Huveneers 2006), *Squalus* (Last *et al.* 2007), and *Mitsukurina*. In addition inter- and intra-specific genetic relationships among species of the genus *Centrophorus* were further investigated by sequencing two gene fragments of mitochondrial (mt) DNA (16S rRNA and cytochrome B).

Ecological risk assessment

The ecological risk assessment of the chondrichthyan fauna distributed within the range of the SESSF undertaken as part of the present project has five separate components: abundance, trend in relative abundance, catch susceptibility, biological productivity, and trophic position. Each of the five components provides a separate perspective on the sustainability of a species and each component is considered separately in a risk assessment framework, where risk is categorised as low, medium, and high. Risk associated with abundance, trend in relative abundance, and trophic level are each derived from a single metric, whereas biological productivity is derived from two components (an age-related mortality metric and a reproductive metric). Catch susceptibility is derived from four parts (availability, encounterability, selectivity, and post-capture mortality) and presented for each of five fishing methods (otter trawl, shark gillnet, shark hook, automatic longline, and trap or pot). The five components are treated as separate entities that cannot be readily combined to form a smaller number of entities.

Sustainability of dogfish

The sustainability of dogfish is assessed by the five components of the methods developed for ecological risk assessment (abundance, trend in relative abundance, catch susceptibility, biological productivity, and trophic position) as described above. In making this assessment species are categorised as occurring predominantly on the continental shelf (<200 m), the upper continental slope (200–599 m), and lower continental slope (≥600 m).

Results/Discussion

Determination of species lists

Table 1 shows the number of separate species identified by the ISMP that have their distribution mostly within the range of the SESSF, and the number of species known from the scientific literature to occur predominantly within the range of the SESSF, yet not identified by the ISMP during 2000–06. Species identified by the ISMP in small quantities that are distributed mostly outside the range of the SESSF are excluded. This gives 121 species (77 shark species, 36 ray species, and 8 holocephalan species). In Table 1, based on mean annual catch during 2000–06, species are arbitrarily classed as 'rare' where mean annual catch is <1 t, 'sparse' where catch is 1–19 t, 'common' where catch is 20–99 t, and abundant where catch is ≥100 t. The 77 shark species were classed as 33 rare, 25 sparse, 8 common, and 11 abundant; the 36 ray species were classed as 8 rare, 9 sparse, 13 common, and 6 abundant; and the 8 holocephalan species were classed as 2 rare, 5 sparse, and 1 abundant.

Tables 2a, 2b, and 2c list only species classed as abundant or common, but Tables 3, 4, 5, 6 and 7 include a comprehensive list of all species detected by the ISMP or described in the literature as predominantly distributed within the range of the SESSF.

Catch evaluation and trend analysis

Tables 2a (sharks), 2b (rays), and 2c (holocephalans) provide simple summaries of estimates of mean annual catch and risk based on observer-standardised-CPUE trends during 2000–06. Within each of the three depth-categories of continental shelf (<200 m), upper-slope–mid-slope (200–599 m), and lower-slope (≥600 m), the tables identify individually the abundant and common species. Percentage of catch retained by fishers and a measure of risk, based on trend analysis, are presented for each of these species. For most species classed as 'sparse' or 'rare' and for some species classed as 'common', there were insufficient data for trend analysis; models applied using GENMOD in the statistical package SAS did not converge and hence provided an indeterminable result. For most species, the results of trend analysis were 'indeterminable' where the mean annual catch was below ~20 t or below ~500 trawl tows selected for analysis. The only exceptions to this pattern were three holocephalan species—blackfin ghostshark (*Hydrolagus lemurs*), Ogilbys ghostshark (*Hydrolagus ogilbyi*), and southern chimaera (*Chimaera* sp a)—where the models converged but exhibited 'no trend'.

Risk of population decline into the future classed as 'high', 'medium', or 'low' was calculated from standardised CPUE based on post-2000 decline (=mean CPUE 2004–06/mean CPUE 2000–02). Post-2000 decline to ≥0.667 was classed as 'low' risk, post-2000 decline to 0.334–0.666 was classed as 'medium' risk, and post-2000 decline to ≤0.333 was classed as 'high' risk. Post-2000 decline was 'indeterminable' for all rare species, most sparse species, and several 'common' species. For these species, greater coverage of otter trawl in the SESSF by the ISMP or change to the design of the ISMP would be required to provide sufficient statistical power to detect trends in standardised CPUE.

Species of shark on the continental shelf identified at 'medium' risk are school shark (*Galeorhinus galeus*), gummy shark (*Mustelus antarcticus*), common sawshark (*Pristiophorus cirratus*), and Australian angel shark (*Squatina australis*) (Table 2a). School shark, gummy shark and common sawshark, which are taken as target or byproduct species by shark gillnet, have undergone extensive ongoing stock assessment through SharkRAG and are now effectively carefully managed by a total allowable catch with individual transferable quota, a narrow mesh-size range (6–6½ inches) for shark gillnet, and closed areas (including nursery areas). For Australian angel shark, the region of medium risk from the effects of otter trawl is restricted to waters off New South Wales (Table 2a). Although the species is exposed to shark gillnet throughout the rest of southern Australia on the continental shelf, shark gillnets take a negligible catch (Walker and Gason 2005) and provide negligible risk.

Species of shark on the upper-slope–mid-slope and lower-slope identified at 'high' or 'medium' risk are whitefin swell shark (*Cephaloscyllium* sp a), greeneye spurdog (*Squalus chloroculus* syn. *mitsukurii*), gulper sharks (*Centrophorus* spp), brier shark (*Deania calcea*), and black shark (*Dalatias licha*) (Table 2a). Analyses for the gulper sharks—mostly *Centrophorus moluccensis* and *C. zeehani* (syn. *C. uyato*), with negligible quantities of *C. harrisson*i—are at higher risk in the western region than in the eastern region of the SETF.

The rays are distributed mostly on the continental shelf and at 'low' risk from the effects of otter trawl. Three species are at 'medium risk': greenback stingaree (*Urolophus viridis*), sandyback stingaree (*U. bucculentus*), and sparsely spotted stingaree (*U. paucimaculatus*) (Table 2b).

Species of holocephalan are mostly distributed on the continental slope, with only the elephant fish (*Callorhinchus milii*) distributed on the continental shelf. Catches are low and insufficient to detect statistically significant trends (Table 2c).

Independent data indicate that most stock depletions occurred before introduction of the ISMP. Trawl surveys by the NSW Fisheries Research Institute during 1977 and 1997 showed a reduction in catch rates of *Centrophorus* spp of 98.4–99.7% (Andrew *et al.* 1997; Graham *et al.* 2001). Examination of research data, fishery catches, and market sales as part of FRDC Project 98/108 shows that dogfish catches taken from the upper slope have not been sustainable. In addition, current assessments indicate that the mature biomass of school shark (*Galeorhinus galeus*) is 12–18% of the pre-fishing levels (Punt *et al.* 2000).

Biological productivity

To determine 'biological productivity' and 'trophic position' more than 15 000 chondrichthyan animals were collected and dissected as part of the present study. These dissections together with about 5000 animals (principally dogfish) collected and dissected through CSIRO as part of FRDC Project 1998/108 provide a total of about 20 000 animals from more than 81 species. For each dissected animal, various biological variables (length, mass, and reproductive indices and measurements) were recorded; vertebrae or dorsal fin-spines were removed and frozen for subsequent laboratory analysis for age determination; and stomach contents, where available, were removed, preserved and analysed in the laboratory to determine trophic position.

In the available data, sample size tends to be larger for abundant species than for rare species. For many of the rare species or species taken in very low numbers in the SESSF, it was not possible to collect sufficient animals to determine the biological parameters. Similarly, it was not possible to collect large numbers of large animals of highly priced species because of cost.

Estimates of maximum age and, where sufficient data were collected, von Bertalanffy growth parameters, with ageing method and reference are presented for each species in Table 3. There is no known method for ageing sixgill and sevengill sharks (order Hexanchiformes) or angels sharks (Squatiniformes) and no further attempt will be made to age these species. Species of dogfish (Squaliformes), catsharks and carpet sharks (Orectolobiformes), and electric rays (Torpediniformes) are very difficult to age and although some were successfully aged as part of the present study, adequate methods were not developed for several species.

Generally, the longest-lived species are the dogfishes and holocephalans (Holocephaliformes) and are classed at very high risk; they can withstand only very limited additional mortality, indicative of low biological productivity. Generally at high risk are the catsharks, carpet sharks, and wobbegongs (Orectolobiformes), mackerel and thresher sharks (Lamniformes), and horn sharks (Heterodontiformes). No species were classed as low risk, but the species generally classed at medium or medium–high risk are the whaler, hammerhead, and smoothhound sharks (Carcharhiniformes), sawsharks (Pristiophoriforrmes), skates (Rajiformes), and eagle devil rays, stingrays, and stingarees (Myliobatiformes).

Estimates of reproductive output are presented in Table 4.

Catch susceptibility

Estimates of 'catch susceptibility' and its four parts 'availability', 'encounterability', 'selectivity', and 'post-capture mortality' for each of 121 species of chondrichthyan species are presented in Table 5 for each of the five major fishing methods of the Southern and Eastern Scalefish and Shark Fishery (SESSF). These five methods are demersal trawl, shark gillnet, shark longline, automatic longline, and trap.

A total of 23 species are identified as high risk under catch susceptibility: Hexanchiformes (1 from automatic longline), Squaliformes (5 from otter trawl and automatic longline), Pristiophoriformes (1 from shark gillnet), Carcharhiniformes (3 from shark gillnet), and Holocephaliformes (8 from otter trawl and 1 from shark gillnet).

Trophic position

Trophic level ranges from 3.25 for the southern eagle ray (*Myliobatus australis*) to 4.55 for broadnose sevengill shark (*Notorhynchus cepedianaus*). Most species of sharks (Selachii) range 4.10–4.50, whereas most species of rays (Batoidea) range 3.25–4.00 and of holocephalans (Holocephalii) range 3.63–4.00 (Table 6).

Chondrichthyan species prey on a wide range of prey, but sharks with trophic levels 4.00–4.25 prey mostly on teleosts and cephalopods and the very few species with trophic levels 4.25–4.55 prey also on mammals, birds, reptiles and other chondrichthyan species. Species of sharks, rays, and holocephalans with trophic levels 3.25–4.00 prey predominantly on crustaceans, molluscs, and other invertebrates.

Among the sharks (Selachii), the highest trophic levels are exhibited by demersal species of Lamniformes at 4.20–4.53. Pelagic and semipelagic species of shark (Lamniformes and Carcharhiniformes) and deep water species (largely Hexanchiformes and Squaliformes) range 4.03–4.55, except for a single species of Squaliformes—the white spotted spurdog (*Squalus acanthias*)—sampled mainly inshore which has a trophic level of 3.70. Angel sharks (Squatiniformes) and wobbegong sharks (family Orectolobidae) as ambush feeders have a similar trophic level at 4.21–4.29. The whaler and hammerhead sharks (Carcharhiniformes) range 3.96–4.23. Other than *S. acanthias*, the only species of shark with trophic levels below 4.00 are the Port Jackson shark (*Heterodontus portusjacksoni*) (Heterodontiformes) (3.46), the rusty carpet shark (*Parascyllium ferrugineum*) (family Parascyllium) (3.51), the orange spotted catshark (*Asymbolus rubiginosus*) (family Scyliorhinidae) (3.85), and the gummy shark (*Mustelus antarcticus*) (family Triakidae) (3.96).

In the present study, only sharks occupy trophic levels >4.25 classed as high risk (11 species); most shark species occupy a trophic level ranging 4.00–4.25 classed as medium risk (31 species), with few occupying a trophic level <4.00 classed low risk (5 species). Rays mostly occupy trophic levels classed as low risk (15 species), with a few classed as medium risk (5 species). All holocephalans occupy trophic levels classed as low risk (6 species), with the exception of a single species classed as medium risk (Table 7).

Species studied in detail such as *Squalus megalops* (Braccini *et al.* 2005) and *Mustelus antarcticus* (Walker 1986) are opportunistic predators that consume a wide range of prey items. When importance of prey was measured by any one of mass or number of prey items, or frequency of occurrence of prey items large regional, seasonal, and ontogenetic differences in dietary composition were found, but there were no differences between mature and immature sharks or between males and females. The spatial and temporal variation in diet exhibited by *S. megalops* and the intrinsic natural variability of the dietary composition of this predator suggest that studies that infer predator-prey interactions from overall diet are likely to miss information on the ecological relationships among species and thus account for only part of these interactions (Braccini *et al.* 2005).

Two sympatric skate species (*Dipturus* sp. B and *D. gudgeri*) from the continental slope, and four sympatric species (*Dipturus* sp. A, *D. cerva*, *D. lemprieri* and *D. whitleyi*) from the continental shelf region were also studied in detail (Treloar *et al.* 2007). These species exhibit variations in feeding strategies that exploit different food sources. The slope assemblage consists of specialised feeders, where *Dipturus* sp. B targets anomurans and a particular species of brachyuran, whereas the diet of *D. gudgeri* consists of mainly teleosts. This feeding strategy could be influenced by less abundant and less diverse food resources in the deeper environment, or abundances of one species out-competing other species. Spatial and seasonal factors may contribute to resource partitioning, but there are no indications of seasonal variability in fish diet on the continental slope and food is recognised as the commonly partitioned resource in marine fish environments. Within the shelf species, the prey groups exploited are diverse comprising of crustaceans, octopus, chondrichthyans, and teleosts. Limited prey items are shared among the species suggesting partitioning of prey resources with skate body size being a contributing factor. Resource partitioning among these species may also be due to morphological attributes developing independently because of prey use and environmental conditions, allowing several species to use similar habitats (Treloar *et al.* 2007).

Resolving taxonomic uncertainty

Genus *Centrophorus*

Application of morphological, morphometric, and meristic methods in the past suggested the presence of four species of gulper shark in Australian waters: Harrison's dogfish (*Centrophorus harrissoni*), southern dogfish (*C. uyato*), leafscale gulper shark (*C. squamosus*), and endeavour dogfish (*C. moluccensis*) (Last and Stevens 1994). More recently, in addition to application of these methods, including placoid scale morphology, CSIRO Marine and Atmospheric Research explored the inter- and intra-specific genetic relationships among these four species of *Centrophorus* by sequencing two gene fragments of mitochondrial (mt) DNA (16S rRNA and cytochrome B). These species appeared not to be endemic to Australia, although sequencing other gene fragments could potentially reveal structuring within these species. This work show different forms of *C. uyato* in the Philippines, Indonesia, New Zealand, Norfolk Ridge, Japan, Australia and the Atlantic (Peter Last, personal observations). Sequencing mtDNA of gene fragments from specimens formerly thought to be *C. uyato* in other parts of the world provided evidence that *C. uyato* should be split into two species (*C. uyato* and *C. zeehani*), where C. *zeehani* is endemic to Australia and *C. uyato* is absent from Australia. *Centrophorus uyato* had previously been described as having an Atlantic and Indo-Pacific distribution and *C. moluccensis* an Indo-Pacific distribution. Overseas studies have been initiated into the systematics of other *Centrophorus* species because of similar concerns. This work indicates that presently only three species of the genus *Centrophorus* occur in Australia: Harrisons dogfish (*Centrophorus harrissoni*), southern dogfish (*C. zeehani*), and endeavour dogfish (*C. moluccensis*). *Centrophorus squamosus* is no longer recognised as a species for Australia.

Genus Squalus

Application of morphological, morphometric, and meristic methods indicate that, within the genus *Squalus*, Australian specimens of *Squalus mitsukurii* differ from the type specimens from Japan and the Australian species is probably a southern endemic. The southern Australian species is now named *Squalus chloroculus* (Last *et al.* 2007). In addition, based on its biogeography, *Squalus megalops* may well be represented by more than one species in Australia.

Genus *Orectolobus*

Two species of the genus *Orectolobus* (*O. ornatus* and *O. maculates*) were described for temperate eastern Australia, but it had been considered that other closely related species may also be present. The subspecies *O. ornatus halei* in southern Australia and *O. ornatus ornatus* in north-eastern waters had been distinguished by differences in colour pattern and the form of the tentacles around the head. This difference between small and large morphs of *O. ornatus* was observed by Last and Stevens (1994), but the taxonomy remained unresolved until recently when sufficient research material became available to apply morphological, morphometric, and meristic methods (Huveneers 2006).

Two closely related species *Orectolobus* (Orectolobidae)—*O. ornatus* (De Vis) and *O. halei* Whitley—were redescribed based on fresh material from temperate eastern Australia. Although described as a subspecies (Whitley 1940), *O. halei* was formerly synonymised with *O. ornatus* because of the lack of research material to assess their conspecificity. Due to its smaller size, *O. ornatus* was previously thought to be the juvenile form of the larger *O. halei*. *Orectolobus ornatus* occurs from Port Douglas in Queensland to Sydney in New South Wales, whereas *O. halei* occurs from Southport in Queensland around the southern coast to Norwegian Bay in Western Australia. *Orectolobus ornatus* differs from *O. halei* in colour pattern, a smaller adult size, fewer dermal lobes at the posterior preorbital group, lower vertebral and spiral valve counts, and the absence of supraorbital knob. Morphometrically, *O. ornatus* has a longer pelvic fin to anal fin interspace, smaller pectoral fins, smaller head dimensions, and relatively smaller claspers in mature specimens (Huveneers 2006).

Genus Mitsukurina

In addition to the goblin shark (*Mitsukurina owstoni*), there is evidence of another species in the genus *Mitsukurina*.

Ecological risk assessment

The present ecological risk assessment draws on information from several sources. Information on catch susceptibility, biological productivity, and trophic position is provided largely from the present project or, for some species, the scientific literature. Information on trend in relative abundance and abundance is based on catch evaluation for the shark gillnet sector of the GHATF (FRDC Project 1999/103) (Walker and Hudson 2005b) and for other sectors of the SESSF (FRDC Project 2001/007) (Walker and Gason 2007).

Of the 23 species identified as high risk under catch susceptibility, 13 are also at high risk from other sources (see Table below). These species belong to the order Hexanchiformes (1 species from automatic longline), Squaliformes (7 species from otter trawl of which 3 are also from automatic longline), Pristiophoriformes (1 species from shark gill net), Squatiniformes (1 species from otter trawl), Carcharhiniformes (3 species from shark gillnet), and Holocephaliformes (8 species from otter trawl and 1 from shark gillnet).

Risk values for species where there is high catch susceptibility

Order	Scientific name	Common name	Risk value for each of three methods and other components						
			Otter trawl	Shark gillnet	Auto long-line	Abun-dance	Trend	Biol-ogical produ-ctivity	Trophic level
Hexanchiformes	*Heptranchias perlo*	Sharpnose sevengill shark	M	L	H	M			M
Squaliformes	*Oxynotus bruniensis*	Prickly dogfish	H	L	L	M			
	Centrophorus harrissoni	Harrissons dogfish	H	L	H	H	H	H	M
	Centrophorus moluccensis	Endeavour dogfish	H	L	H	L	H	H	M
	Centrophorus zeehani	Southern dogfish	H	L	H	M	H	H	M
	Centroscyllium kamoharai	Bareskin dogfish	H	L	H	H			M
	Deania quadrispinosa	Longsnout dogfish	H	L	L	M			M
	Squalus chloroculus	Green-eyed spurdog	H	L	H	L	H	H	H
Pristiophoriformes	*Pristiophorus cirratus*	Common sawshark	L	H	L	L	M	M	
Squatiniformes	*Squatina sp A*	Eastern angel shark	H	L	L	M			M
Carcharhiniformes	*Furgaleus macki*	Whiskery shark	L	H	L	L		M	M
	Galeorhinus galeus	School Shark	L	H	L	L	M	H	M
	Mustelus antarcticus	Gummy Shark	L	H	L	L	M	M	L
Holocephaliformes	*Callorhinchus milii*	Elephant fish	L	H	L	L		H	L
	Chimaera lignaria	Giant chimaera	H	L	L	H		H	L
	Chimaera sp A	Southern chimaera	H	L	M	M	H	H	L
	Hydrolagus	Blackfin	H	L	M	M	L		L

	lemures	ghostshark							
	Hydrolagus ogilbyi	Ogilbys ghostshark	H	L	M	M	L	H	M
	Hydrolagus sp A	Black ghostshark	H	L	L	H			L
	Hydrolagus sp C	Giant ghostshark	H	L	L	H			L
	Harriotta raleighana	Bigspine spookfish	H	L	L	H			
	Rhinochimaera pacifica	Pacific spookfish	H	L	L	H		H	L

Sustainability of dogfish

The species at highest risk occur in the upper continental shelf region. Species identified as having their populations markedly reduced from the effects of fishing and requiring special rehabilitation are the gulper sharks (*Centrophorus* spp) and the greeneye spurdog (*Squalus chloroculus* syn. *mitsukurii*). Catches of these species and the other deepwater species of dogfish *Centroscymnus owstoni*, *Deania calcea*, and *Dalatias licha* are controlled by trip limits. The species are partly controlled by a basket trip limit for dogfish to prevent fishers from targeting these species. A temporary closed area for gulper sharks and *Galeorhinus galeus* was presently established on the continental slope off Kangaroo Island in South Australia. However, following survey of the waters off South Australia and Western Australia by automatic longline fishing to assess their suitability for closed areas for gulper sharks and *Galeorhinus galeus* resulted in dismantling this closure and establishing one further west.

Various updates of the results of the analyses presented in this report and a separate report on scalefish (Walker *et al.* 2007) have been presented to AFMA. The results have provided an important input to the decision making processes associated with setting basket quotas for dogfish and holocephalans, and for establishing spatial closures during June 2007. Many of these spatial closures are targeted at improved management of school shark through protection of breeding animals and of gulper sharks through four gulper shark closures. Deepwater dogfish and holocephalans will receive additional protection through the closure of all waters of depth greater than 700 m in the SETF.

Benefits and Adoption

The direct benefits from the present project flow to the GHATF (35%), SETF (35%), GABTF (10%), and each of the south-eastern States of Victoria (5%), Tasmania (5%), South Australia (5%), and New South Wales (5%). While direct benefits flow to the commercial fisheries, new information on chondrichthyan species from the project indirectly benefit AFMA, DAFF, DEWR, the State fisheries agencies, and the recreational fishing sector.

The results of assessment of sustainability feed into several regional, national, and international fishery-management processes. (1) AFMA is required to provide data and data synthesis to resource assessment groups and fishery management committees involving industry, scientist, and fishery managers associated with the SESSF. (2) DEWR requires under the Commonwealth EPBC Act 1999 a Strategic Environmental Impact Assessment for each Commonwealth managed fishery and each export State-managed fishery. (3) DEWR requires under the EPBC Act 1999 identification of threatened and potentially threatened marine and estuarine fishes. (4) AFMA is required to update periodically a Bycatch Action Plan for each major Commonwealth managed fishery under Australia's Fisheries Management Act 1991. (5) AFMA is required to respond to the Commonwealth Fisheries Minister's direction of December 2005 to cease overfishing and to halve bycatch. (6) DAFF is required to address Australia's international obligation to update periodically the national Shark Assessment Report and Shark Plan, which form Australia's National Plan of Action for the Management and Conservation of Sharks (NPOA-Sharks). As a signatory nation to the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks), developed by the United Nations Food and Agriculture Organisation (FAO), Australia is required to provide these documents periodically to the FAO Committee of Fisheries (COFI). (7) The State fisheries agencies are required to meet their obligations under the NPOA-Sharks, and to update periodically the State chapters of the national Shark Assessment Report and to update the Shark Plan. (8) Several State fisheries agencies are required to update State Bycatch Action Plans.

The report for FRDC Project 2001/007 focussing on sharks, rays and holocephalans (Walker and Gason 2007) and a separate report focussing on other groups (Walker *et al.* 2007) together provide the most comprehensive analysis of the data collected by the Integrated Scientific Monitoring Program (ISMP) since it began in 1992. The results of the trends in relative abundance (standardised CPUE) and evaluated catches presented in these two reports combined with available results on biological productivity and catch susceptibility from the present project have been variously presented to AFMA, CSIRO, SharkRAG, and several industry forums. This package of results has been and continues to be a major input to the decision-making processes associated with setting basket quotas for dogfish and holocephalans, and for establishing spatial closures during June 2007. Many of these spatial closures improve management of school shark (*Galeorhinus galeus*) through protection of breeding animals and of gulper shark (*Centrophorus* spp) and greeneye spurdog (*Squalus chloroculus*) through four gulper shark closures. Deepwater dogfish and holocephalans are receiving additional protection through the closure of all waters of depth greater than 700 m in the SETF and some of the other initiatives undertaken as part of the recent structural adjustment of the SESSF.

Rapid assessment from the present FRDC project and FRDC Project 2000/007 provide a comprehensive basis for ecological risk assessment of all species of chondrichthyan species where catches exceed 20 t a year from across the SESSF.

Following documentation of the results from the present project, most future work will relate to periodic assessment of bycatch and ecological risk assessment in the SESSF and other Commonwealth and State fisheries and updating of the Shark Assessment Report associated with Australia National Plan of Action for the Conservation and Management of Sharks. All data are managed in accessible databases in SAS. As these data sets are updated, they can be made available as required.

Further Development

The present project contributed to enhancing methods for ageing and determining key demographic parameters for chondrichthyan species. In addition, the present project initiated building strong collaborative partnerships between MAFFRI and universities and between CSIRO and universities. The formation of these partnerships has created a momentum persisting well beyond the duration of the present project. Already several projects funded from alternative sources are under way to extend methods developed and to address questions raised by the present project. For example, a current collaborative project between MAFFRI and Monash University funded as an ARC Linkage Grant is measuring post-capture fishing mortality on several important chondrichthyan species through simulation of gillnet, hook, and trawl fishing under experimental conditions. Work is continuing to refine methods of ageing for species considered difficult to age and to refine understanding of the reproductive biology of these species.

A major output from the present project, drawing on the results from FRDC Project 2000/007, is that there are 121 species distributed predominantly in southern Australia detected by the ISMP or described in the literature (Walker and Gason 2007). Of these, only 18 species are abundant (≥100t annual catch) and 21 species are common (20–99 t annual catch). There are 39 species classed as sparse (1–19 t annual catch) and 43 species classed as rare (< 1 t annual catch). The implication for the present project is that it was logistically difficult or impossible to collect sufficient material for many species to determine their demographic parameters.

Results from the present project are gradually becoming available to scientists, fishery managers, industry personnel, and other beneficiaries in the form of the present report final to FRDC and a large number of scientific outputs. The scientific outputs presently includes 14 papers published, 1 paper in press, and 2 papers submitted in internationally peer reviewed scientific journals, 4 chapters published in peer reviewed books, and 6 Ph.D. theses and 8 B.Sc. (Hons) theses. There are presently a further 6 Ph.D. theses in preparation. Many more papers on completed work will be submitted for publication in scientific journals in the months ahead. Publishing the results in journal papers and presenting the results at scientific conferences ensures rigorous peer review of the work and accessibility to the scientific community.

Planned Outcomes

Assessment of the sustainability of individual chondrichthyan species in southern Australia was undertaken through rapid assessment of ecological risk from effects of fishing using a framework involving five components. This framework involved combining the results for three components determined by the present project with the results for two components determined by the recently completed FRDC Project 2000/007 titled 'Shark and other chondrichthyan byproduct and bycatch estimation in the Southern and Eastern Scalefish and Shark Fishery' (Walker and Gason 2007). The three components determined by the present project are biological productivity, catch susceptibility, and food web trophic position, and the two components determined by FRDC Project 2000/007 are evaluated catch and relative abundance trend. All five components apply to each species, but, in addition, evaluated catch and catch susceptibility also apply to each of five fishing methods (otter trawl, shark gillnet, shark longline, automatic longline, and trap or pot.

The results of assessment of sustainability feed into several regional, national, and international fishery-management processes. (1) AFMA is required to provide data and data synthesis to resource assessment groups and fishery management committees involving industry, scientist, and fishery managers associated with the SESSF. (2) DEWR requires under the Commonwealth EPBC Act 1999 a Strategic Environmental Impact Assessment for each Commonwealth managed fishery and each export State-managed fishery. (3) DEWR requires under the EPBC Act 1999 identification of threatened and potentially threatened marine and estuarine fishes. (4) AFMA is required under Australia's Fisheries Management Act 1991 a Bycatch Action Plan for each major Commonwealth managed fishery. (5) AFMA is required to respond to the Commonwealth Fisheries Minister's direction of December 2005 to cease overfishing and to halve bycatch. (6) DAFF is required to address Australia's international obligation to update periodically the national Shark Assessment Report and Shark Plan, which form Australia's National Plan of Action for the Management and Conservation of Sharks (NPOA-Sharks). As a signatory nation to the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks), developed by the United Nations Food and Agriculture Organisation (FAO), Australia is required to report periodically these documents to the FAO Committee of Fisheries (COFI). (7) The State fisheries agencies are required to meet their obligations under the NPOA-Sharks, and to update periodically the State chapters of the national Shark Assessment Report and to update the Shark Plan. (8) Several State fisheries agencies are required to update State Bycatch Action Plans.

The report for FRDC Project 2007 focussing on sharks, rays and holocephalans (Walker and Gason 2007) and a separate report focussing on other groups (Walker *et al.* 2007) together provide the most comprehensive analysis of the data collected by the Integrated Scientific Monitoring Program (ISMP) since it began in 1992. The results of the trends in relative abundance (standardised CPUE) and evaluated catches presented in these two reports combined with available results on biological productivity and catch susceptibility from the present project have been variously presented to AFMA, CSIRO, SharkRAG, and several industry forums. This package of results have been and continues to be a major input to the decision-making processes associated with setting basket quotas for dogfish and holocephalans, and for establishing spatial closures during June 2007. Many of these spatial closures improve management of school shark (*Galeorhinus galeus*) through protection of breeding animals and of gulper shark (*Centrophorus* spp) and greeneye spurdog (*Squalus mitsukuri*) through four gulper shark closures. Deepwater dogfish and holocephalans will receive additional protection through the closure of all waters of depth greater than 700 m in the SETF and some of the other initiatives undertaken as part of the recent structural adjustment of the SESSF.

In addition to providing results immediately applicable for rapid assessment of ecological risk and fishery management, the present project provides facility for rapid data retrieval and update of statistical analyses as required for estimating demographic parameters. Data and specific analyses can be provided readily to other scientists and fisheries mangers as required.

As AFMA and the Commonwealth Management Advisory Committees recognise the need for a more integrated approach to management across the south-eastern fisheries, the package of results from the present project and FRDC Project 2000/007 will be gradually incorporated into broad-scale ecosystem models such as "Atlantis" in southern Australia.

Conclusion

Rapid assessment of sustainability for ecological risk to the chondrichthyan species of southern Australia taken in the SESSF using the five components of abundance, relative abundance trend, biological productivity, catch susceptibility, and trophic position provides a valuable framework for management and conservation mitigation and priorities for further research.

Three species of gulper shark (*Centrophorus harrissoni*, *C. moluccensis*, and *C. zeehani*) and greeneye spurdog (*Squalus chloroculus*) are at highest risk from the effects of fishing because of their low biological productivity and abundance trend, and *C. harrissoni* is now rare and *S. chloroculus* has high trophic level. Three other dogfish—prickly dogfish *Oxynotus bruniensis*), bareskin dogfish (*Centroscyllium kamoharai*), and longsnout dogfish (*Deania quadrispinosa*)—are likely to all have low biological productivity, and *C. kamoharai* is rare. School shark (*Galeorhinus galeus*) and all holocephalans have low biological productivity and four of the holocephalan species—black ghostshark (*Hydrolagus* sp *A*), giant ghostshark (*Hydrolagus* sp *C*), bigspine spookfish (*Harriotta raleighana*), and Pacific spookfish (*Rhinochimaera pacifica*)—are rare. The closure of waters >700 m will provide for improve management of many species of dogfish and holocephalans, but will provide little benefit to the gulper sharks and greeneye spurdog, which inhabit the upper- and mid-slope. The upper- and mid-slope species will receive benefit from implementation of closed areas.

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Table 1. Number of species by abundance category and depth range

Reproduced from final report for FRDC Project 2000/007 (Walker and Gason 2007). Abundance category is mostly total catch in the SESSF: rare <1 t; sparse, 1–19 t; common 20–99 t; abundant, ≥100 t. Except for common cosmopolitan species, species distributed predominantly outside the range of the SESSF are excluded from present study and report.

Abundance category	Number of species			
	Shelf <200 m	Upper-mid slope 200–599 m	Deep-water ≥600 m	Total
Sharks (Selachii)				
Rare	11	13	9	33
Sparse	11	9	5	25
Common	3	2	3	8
Abundant	7	3	1	11
Total	32	27	18	77
Rays (Batoidea)				
Rare	5	2	1	8
Sparse	7	2	0	9
Common	11	2	0	13
Abundant	6	0	0	6
Total	29	6	1	36
Holocephalans (Holocephalii)				
Rare	0	0	2	2
Sparse	0	3	2	5
Common	0	0	0	0
Abundant	1	0	0	1
Total	1	3	4	8
Grand total	62	36	23	121

Source: MAFFRI Queenscliff Centre, DIMSAS-SESSF, ISMP 22 January 2007

Table 2a. Summary data for species of shark (selachii) by abundance category and depth range

Reproduced from report on FRDC Project 2000/007 (Walker and Gason 2007). Shark gillnet and shark longling catch is included in SESSF quota, but not included in ISMP catch estimate. Abundance category is based on mostly total catch in the SESSF: rare <1 t; sparse, 1–19 t; common 20–99 t; abundant, ≥100 t; risk category is derived from standardised CPUE based on post-2000 decline (=mean cpue 2004–06/mean cpue 2000–02): low, ≥0.667; medium, 0.334–0.666; high, ≤0.333.

Common name	Scientific name	ISMP[A] catch estimate	Per cent retained	Abundance category	Trend	Post-2000 decline	Risk	Management mitgation
Continental shelf (<200 m)								
School shark	*Galeorhinus galeus*	35		Abundant	Decline only	0.426	Medium	Quota (257 t)[B]
Gummy shark	*Mustelus antarcticus*	185	94	Abundant	Rise-peak-decline	0.520	Medium	Quota (1800 t)
Australian angel shark	*Squatina australis*	313	97	Abundant	Rise-peak-decline	0.657	Medium	
Ornate angel shark	*Squatina tergocellata*	289	75	Abundant	Rise-peak-decline	1.643	Low	
Common sawshark	*Pristiophorus cirratus*	280	93	Abundant	Rise-peak-decline	0.556	Medium	Quota (434 t)[C]
Port Jackson shark	*Heterodontus portusjacksoni*	211	0	Abundant	Rise-peak-decline	0.687	Low	
Draughtboard shark	*Cephaloscyllium laticeps*	227	47	Abundant	No trend	0.864	Low	
Grey-spotted catshark	*Asymbolis analis*	26	0	Common	No trend	0.675	Low	
Southern sawshark	*Pristiophorus nudipinnis*	32	96	Common	Indeterminable			Quota[C]
Spotted wobbegong	*Orectolobus maculatus*	24	89	Common	Indeterminable			
11 sparse species (4 included from inshore fisheries)		1–19		Sparse	Indeterminable			
11 rare species (3 from literature)		<1		Rare	Indeterminable			
Upper-slope–mid-slope (200–599 m)								
Spikey spurdog	*Squalus megalops*	719	28	Abundant	Rise only	2.643	Low	Spatial closure
Whitefin swellshark	*Cephaloscyllium* sp a	385	10	Abundant	Rise-peak-decline	0.508	Medium	Spatial closure
Greeneye spurdog	*Squalus mitsukurii*	112	24	Abundant	Rise-peak-decline	0.123	High	Spatial closure
Gulper shark	*Centrophorus spp* [D]	56	75	Common	No trend	0.273	High[E]	Spatial closure
Sawtail shark	*Galeus boardmani*	23	0	Common	Decline	0.903	Low	
9 sparse species		1–19		Sparse	Indeterminable			
13 rare species (4 from literature)		<1		Rare	Indeterminable			
Lower-slope (≥600 m)								
Brier shark	*Deania calcea*	257	81	Abundant	Decline	0.476	Medium	Closure >700 m
Platypus shark	*Deania* spp	97	93	Common	Indeterminable			Closure >700 m
Black shark	*Dalatias licha*	81	45	Common	Decline	0.204	High	Closure >700 m
Owstons shark	*Centroscymnus owstoni*	71	93	Common	Decline	1.578	Low	Closure >700 m
Golden dogfish	*Centroscymnus crepidator*	56	93	Common	Indeterminable			Closure >700 m
5 sparse species		1–19		Sparse	Indeterminable			Closure >700 m
9 rare species (2 from literature)		<1		Rare	Indeterminable			Closure >700 m

[A] Excludes shark gillnet and shark longline fishing catch; [B] SESSF quota includes shark gillnet and shark longline fishing catch; [C] sawshark quota; [D] mostly *Centrophorus moluccensis* and *C. uyato* , with negligible quantities of *C. harrissoni* , and *C. squamosus* ; [E] post-2000 decline in western region is 0.273 (high risk), whereas eastern region is 1.667 (low risk).

Source: MAFFRI Queenscliff Centre, DIMSAS-SESSF, ISMP 22 January 2007

Table 2b. Summary data on species of rays (batoidea) by abundance category and depth range

Reproduced from report on FRDC Project 2000/007 (Walker and Gason 2007). Shark gillnet and shark longling catch is included in SESSF quota, but not included in ISMP catch estimate. Abundance category is based on mostly total catch in the SESSF: rare <1 t; sparse, 1–19 t; common 20–99 t; abundant, ≥100 t; risk category is derived from standardised CPUE based on post-2000 decline (=mean cpue 2004–06/mean cpue 2000–02): low, ≥0.667; medium, 0.334–0.666; high, ≤0.333.

Common name	Scientific name	ISMP[A] catch estimate (t)	Per cent retained	Abundance category	Trend	Post-2000 decline	Risk	Management mitigation
Continental shelf (<200 m)								
Greenback stingaree	*Urolophus viridis*	455	0	Abundant	Decline only	0.337	Medium	
Wide stingaree	*Urolophus expansus*	351	0	Abundant	No trend	1.067	Low	
Southern fiddler ray	*Trygonorrhina fasciata*	219	26	Abundant	No trend	1.252	Low	
Melbourne skate	*Dipturus whitleyi*	176	30	Abundant	Rise only	2.233	Low	
Sydney skate	*Dipturus australis*	157	0	Abundant	Rise-peak-decline	0.721	Low	
Sandyback stingaree	*Urolophus bucculentus*	124	19	Abundant	Rise-peak-decline	0.405	Medium	
Black stingray	*Dasyatis thetidis*	96	26	Common	Rise only	2.232	Low	
Sparsely spotted stingaree	*Urolophus paucimaculatus*	90	1	Common	Decline only	0.615	Medium	
Smooth stingray	*Dasyatis brevicaudata*	89	5	Common	Rise-peak-decline	2.123	Low	
Southern eagle ray	*Myliobatis australis*	88	55	Common	No trend	2.077	Low	
Banded stingaree	*Urolophus cruciatus*	70	0	Common	Rise-peak-decline	0.861	Low	
Peacock skate	*Pavoraja nitida*	70	0	Common	No trend	0.873	Low	
Tasmanian numbfish	*Narcine tasmaniensis*	56	0	Common	Rise only	4.715	Low	
Whitespotted skate	*Dipturus cerva*	37	0	Common	Indeterminable			
Common stingaree	*Trygonoptera testacea*	31	0	Common	Indeterminable			
Longnose skate	*Dipturus* sp A	25	67	Common	Indeterminable			
Eastern shovelnose	*Aptychotrema rostrata*	23	77	Common	Rise only	9.555	Low	
7 sparse species		1–19		Sparse	Indeterminable			
5 rare species (3 from literature with zero catch)		<1		Rare	Indeterminable			
Upper-slope–mid-slope (200–599 m)								
Bight skate	*Dipturus gudgeri*	88		Common	Rise only	2.232	Low	
Short-tail torpedo ray	*Torpedo macneilli*	72		Common	Rise-peak-decline	1.067	Low	
2 sparse species		1–19		Sparse	Indeterminable			
2 rare species		<1		Rare	Indeterminable			
Lower-slope (≥600 m)								
0 sparse species		1–19		Sparse				
1 rare species (includes 1 from literature with zero catch)		<1		Rare	Indeterminable			Closure >700 m

Source: MAFFRI Queenscliff Centre, DIMSAS-SESSF, ISMP 22 January 2007

Table 2c. Summary data on species of holocephalans (holocephalii) by abundance category and depth range

Reproduced from report on FRDC Project 2000/007 (Walker and Gason 2007). Shark gillnet and shark longling catch is included in SESSF quota, but not included in ISMP catch estimate. Abundance category is based on mostly total catch in the SESSF: rare <1 t; sparse, 1–19 t; common 20–99 t; abundant, ≥100 t; risk category is derived from standardised CPUE based on post-2000 decline (=mean cpue 2004–06/mean cpue 2000–02): low, ≥0.667; medium, 0.334–0.666; high, ≤0.333.

Common name	Scientific name	ISMP[A] catch estimate	Per cent retained	Abundance category	Trend	Post-2000 decline	Risk	Management mitigation
Continental shelf (<200 m)								
Elephant fish	*Callorhinchus milii*	94	94	Abundant	Indeterminable			Quota (130 t)[B]
0 sparse species		1–19		Sparse	Indeterminable			
0 rare species		<1		Rare	Indeterminable			
Upper-slope–mid-slope (200–599 m)								
Southern chimaera	*Chimaera* sp A	12	89	Sparse	No trend	0.204	High	Quota (basket)
Ogilbys ghostshark	*Hydrolagus ogilby*	10	89	Sparse	No trend	1.870	Low	Quota (basket)
1 sparse species		1–19		Sparse	Indeterminable			Quota (basket)
0 rare species		<1		Rare	Indeterminable			
Lower-slope (≥600 m)								
Blackfin ghostshark	*Hydrolagus lemures*	11	74	Sparse	No trend	1.274	Low	Closure >700 m
1 sparse species		1–19		Sparse	Indeterminable			Closure >700 m
2 rare species		<1		Rare	Indeterminable			Closure >700 m

[A] Excludes shark gillnet and shark longline fishing catch; [B] SESSF quota includes shark gillnet and shark longline fishing catch.

Source: MAFFRI Queenscliff Centre, DIMSAS-SESSF, ISMP 22 January 2007

Table 3. Biological productivity: age and growth

Biological productivity (BP) based on age is classed as L (low >16 years), M (medium 8–16 years), and H (high <8 years). Abundance scale based on SESSF ISMP and logbook catches: abun, abumdant (≥100 t); com, common (20−99 t); spar, sparse (1−19 t); rare, rare (<1 t). Length type: TL, total length; FL, folk length; DW, disc width. nd, no data.

Table 3 (continued)

Scientific name	Common name	Family	Abundance	Length type	Female growth (von Bertalanffy)						Male growth (von Bertalanffy)						Tissue	Count	Growth reference	BP
					No. aged	L_{Max} (mm)	L_{∞} (mm)	K (yr^{-1})	a_0 (yr)	Max age	No. aged	L_{Max} (mm)	L_{∞} (mm)	K (yr^{-1})	a_0 (yr)	Max age				
Pelagic and semipelagic species																				
Lamniformes	Mackerel & thresher sharks																			
Alopias vulpinus	Thresher shark	*Alopiidae*	Spar	TL	23	6500	6360	0.158	–1.02	22	16		4927	0.215	–1.42	16	Vertebra centrum whole	External bands	Cailliet and Bedford (1983)	L
Isurus oxyrinchus	Shortfin mako	*Lamnidae*	Spar	FL	188	3470	8201	0.013	–11.30	28	214		3023	0.052	–9.0	29	Vertebra centrum section	Internal bands	Bishop *et al* . (2006)	L
Lamna nasus	Porbeagle	*Lamnidae*	Rare	FL	291		3100	0.060	–5.90	24	283		2580	0.080	–5.8	25	Vertebra centrum section	Internal bands	Natanson *et al* . (2002)	L
Carcharhiniformes	Whaler & hammerhead sharks																			
Prionace glauca	Blue shark	*Carcharhinidae*	Rare	TL	236	3150	3521	0.157	−1.01	12			♂ & ♀ combined				Vertebra centrum section	Internal bands	Lessa, R. *et al* . (2004)	M
Myliobatiformes																				
Manta birostris	Manta ray	*Mobulidae*	Rare	DW	nd	6700					nd		♂ & ♀ combined						Tricas *et al.* (1997)	
Demersal species																				
Hexanchiformes	Sixgill & sevengill sharks																			
Chlamydoselachus anguineus	Frill shark	*Chlamydoselachidae*	Rare		nd	1960					nd	1650					No known ageing method		Cortés (2000)	
Heptranchias perlo	Sharpnose sevengill shark	*Hexanchidae*	Spar		nd						nd						No known ageing method			
Hexanchus nakamurai	Bigeye sixgill shark	*Hexanchidae*	Rare		nd	4820					nd						No known ageing method		Cortés (2000)	
Hexanchus griseus	Bluntnose sixgill shark	*Hexanchidae*	Rare		nd						nd						No known ageing method			
Notorynchus cepedianus	Broadnose sevengill shark	*Hexanchidae*	Com	TL		2960	3000	0.107		32		2430	2500	0.174		20	Captive sharks		van Dykhuizen and Mollet (1992)	L
Squaliformes	Dogfishes																			
Echinorhinus brucus	Bramble shark	*Echinorhinidae*	Rare		nd						nd									
Oxynotus bruniensis	Prickly dogfish	*Echinorhinidae*	Spar		nd						nd									
Centrophorus harrissoni	Harrissons dogfish	*Squalidae*	Rare	TL	34		944	0.100	0.00	39			♂ & ♀ combined				Second dorsal spine	External bands	Whiteley (2005)	L
Centrophorus moluccensis	Endeavour dogfish	*Squalidae*	Com		nd	930					nd	780							Daley *et al.* (2002)	
Centrophorus zeehani	Southern dogfish	*Squalidae*	Spar	TL	35		898	0.300	0.00	35			♂ & ♀ combined				Second dorsal spine	External bands	Whiteley (2005)	L
Centrophorus zeehani	Southern dogfish	*Squalidae*	Spar	TL	13					36	17					37	Second dorsal spine	External bands	MAFFRI (Unpublished data)	L
Centroscyllium kamoharai	Bareskin dogfish	*Squalidae*	Rare		nd	630					nd	540							Daley *et al.* (2002)	
Centroscymnus crepidater	Golden dogfish	*Squalidae*	Com	TL	146	995	961	0.072	–6.13	54	86	790	732	0.141	–2.99	34	Second dorsal spine	External bands	Irvine (2004)	L
Centroscymnus coelolepis	Portugese dogfish	*Squalidae*	Spar	TL	nd	1130					nd	1000					No known ageing method		Irvine (2004)	
Centroscymnus owstoni	Owstons dogfish	*Squalidae*	Com	TL	6	1160				29	6	940				24	Second dorsal spine	External bands	Irvine (2004)	L
Centroscymnus plunketi	Plunkets dogfish	*Squalidae*	Rare	TL	19	1550				29	19	1290				30	Second dorsal spine	External bands	Irvine (2004)	L
Cirrhigaleus barbifer	Mandarin shark	*Squalidae*	Rare		nd						nd									
Dalatias licha	Black shark	*Squalidae*	Com		nd	1237					nd	1040								
Deania calcea	Brier shark	*Squalidae*	Abun	TL	46	1150	1225	0.051	–5.11	36	16	910	id	id	id	32	Second dorsal spine	External bands	Irvine (2004)	L
Deania quadrispinosa	Longsnout dogfish	*Squalidae*	Spar		nd	1180					nd	960							Daley *et al.* (2002)	
Etmopterus baxteri	Giant lantern shark	*Squalidae*	Rare	TL	158	870	836	0.038	–4.36	58	83	740	646	0.065	–4.36	48	Second dorsal spine	External bands	Irvine (2004)	L
Etmopterus bigelowi	Smooth lantern shark	*Squalidae*	Spar		nd						nd									
Etmopterus granulosus	Southern lantern shark	*Squalidae*	Spar	TL	2	780				14	5	680				19	Second dorsal spine	Internal bands	Irvine (2000)	
Etmopterus lucifer	Blackbelly lantern shark	*Squalidae*	Spar	TL	nd	555					nd	457								
Etmopterus pusillus	Slender Lantern shark	*Squalidae*	Rare	TL		502	540	0.130		17		479	490	0.170		13	Second dorsal spine	Internal bands	Coelho and Erzini (2007)	L
Etmopterus sp A	Bristled latern shark	*Squalidae*	Rare		nd						nd									
Isistius brasiliensis	Cookie-cutter shark	*Squalidae*	Rare		nd						nd									
Somniosus pacificus	Pacific sleeper shark	*Squalidae*	Rare		nd	4300					nd								Ebert *et al.* (1987)	
Squalus acanthias	White-spotted spurdog	*Squalidae*	Spar	TL		788	1253	0.048	-4.9	80		1064	998	0.070	–4.73	38	Second dorsal spine	External bands	Ketchen (1975)	
Squalus chloroculus	Green-eyed spurdog	*Squalidae*	Abun	TL	13	1020				36	44	940				24	Second dorsal spine	External bands	MAFFRI (Unpublished data)	L
Squalus megalops	Spikey spurdog	*Squalidae*	Abun	TL	274	622	829	0.034	–10.83	28	157	470	455	0.144	–5.72	15	First dorsal spine	External bands	Braccini *et al* . (2007)	L
Zameus squamulosus	Velvet dogfish	*Squalidae*	Rare		nd						nd									

Table 3 (continued)

Scientific name	Common name	Family	Abundance	Length type	Female growth (von Bertalanffy)						Male growth (von Bertalanffy)						Tissue	Count	Growth reference	BP
					No. aged	L_{Max} (mm)	L_∞ (mm)	K (yr^{-1})	a_0 (yr)	Max age	No. aged	L_{Max} (mm)	L_∞ (mm)	K (yr^{-1})	a_0 (yr)	Max age				
Pristiophoriformes	Sawsharks																			
Pristiophorus cirratus	Common sawshark	*Pristiophoridae*	Abun	TL	324	1492	1518	0.149	–2.38	15	273	1231	1180	0.290	–1.38	10	Whole vertebra centrum	External bands	Walker *et al*. (2005)	M
Pristiophorus nudipinnis	Southern sawshark	*Pristiophoridae*	Com	TL	203	1235	1054	0.484	–0.60	9	192	1095	977	0.571	–0.75	8	Whole vertebra centrum	External bands	Walker *et al*. (2005)	M
Pristiophorus sp A	Eastern sawshark	*Pristiophoridae*	Spar		nd						nd									
Squatiniformes	Angel sharks																			
Squatina australis	Australian angel shark	*Squatinidae*	Abun	TL	nd	1160					nd	998					No known ageing method		MAFFRI (Unpublished data)	
Squatina tergocellata	Ornate angel shark	*Squatinidae*	Abun		nd						nd						No known ageing method			
Squatina sp A	Eastern angel shark	*Squatinidae*	Spar	TL	nd	1220					nd	939					No known ageing method		MAFFRI (Unpublished data)	
Heterodontiformes	Horn sharks																			
Heterodontus galeatus	Crested horn shark	*Heterodontidae*	Rare		nd						nd									
Heterodontus portusjacksoni	Port Jackson shark	*Heterodontidae*	Abun	TL	79	1225	1242	0.070	3.86	35	100	1103	1080	0.084	4.086	28	First dorsal-fin spine	Inner trunk dentine layer	Tovar-Ávila *et al.* (submitted)	L
Orectolobiformes	Catsharks, wobbegongs, carpet																			
Brachaelurus waddi	Blind Shark	*Brachaeluridae*	Rare		nd						nd									
Orectolobus halei	Ornate wobbegong	*Orectolobidae*	Abun	TL	188	2015	2401	0.090	4.66	27		2065	♂ & ♀ combined				Vertebra centrum section	Internal bands	Huveneers (2007)	L
Orectolobus maculatus	Spotted wobbegong	*Orectolobidae*	Abun	TL	120	1510	1722	0.090	–1.12	22		1575	♂ & ♀ combined				Vertebra centrum section	Internal bands	Huveneers (2007)	L
Orectolobus ornatus	Dwarf wobbegong	*Orectolobidae*	Com	TL	201	1017	1099	0.100	–1.09	20		995	♂ & ♀ combined				Vertebra centrum section	Internal bands	Huveneers (2007)	L
Sutorectus tentaculatus	Cobbler wobbegong	*Orectolobidae*	Rare		nd															
Parascyllium collare	Collared carpet shark	*Parascylliidae*	Rare		nd															
Parascyllium ferrugineum	Rusty carpet shark	*Parascylliidae*	Spar		nd	890					nd	710					No known ageing method		MAFFRI (unpublished data)	
Parascyllium variolatum	Varied carpet shark	*Parascylliidae*	Rare		nd															
Apristurus sp A	Freckled catshark	*Scyliorhinidae*	Rare		nd															
Apristurus sp C	Fleshynose catshark	*Scyliorhinidae*	Rare		nd															
Apristurus sp D	Roughskin catshark	*Scyliorhinidae*	Rare		nd	832						872					No known ageing method		CSIRO (unpublished data)	
Apristurus sp E	Bulldog catshark	*Scyliorhinidae*	Rare		nd															
Apristurus sp G	Pinocchio catshark	*Scyliorhinidae*	Rare		nd	820						825					No known ageing method		CSIRO (unpublished data)	
Asymbolus analis	Grey spotted catshark	*Scyliorhinidae*	Com																	
Asymbolus occiduus	Western spotted catshark	*Scyliorhinidae*	Rare																	
Asymbolus rubiginosus	Orange spotted catshark	*Scyliorhinidae*	Rare		nd						nd						No known ageing method		MAFFRI (unpublished data)	
Asymbolus vincenti	Gulf catshark	*Scyliorhinidae*	Rare																	
Cephaloscyllium laticeps	Draughtboard shark	*Scyliorhinidae*	Abun		nd						nd						No known ageing method		Awruck *et al* (in prep)	
Cephaloscyllium sp A	Whitefinned swell shark	*Scyliorhinidae*	Abun	TL	81	1174	1154	0.100	–4.86	27	37	1127	1089	0.140	–2.70	20	Whole vertebra centrum	External bands	Bell (in preparation)	L
Galeus boardmani	Sawtail shark	*Scyliorhinidae*	Com		nd	587						510					No known ageing method		CSIRO (unpublished data)	
Lamniformes	Mackerel & thresher sharks																			
Carcharidon carcharias	White shark	*Lamnidae*	Rare		112	6100	6860	0.065	–4.40	13	nd		♂ & ♀ combined				Whole vertebra centrum	External bands	Wintner (1999)	M
Mitsukurina owstoni	Goblin shark	*Mitsukurinidae*	Rare		nd						nd									
Carcharias taurus	Grey nurse shark	*Odontaspididae*	Rare	TL	48	3180	2958	0.110	–4.2	17	48	2500	2495	0.16	–3.4	15	Vertebra centrum section	Internal bands	Goldman *et al.* (2006)	L
Odontaspis ferox	Smalltooth sandtiger shark	*Odontaspididae*	Rare		nd						nd									
Carcharhiniformes	Whaler, hammerhead & smoothhound sharks																			
Carcharhinus brachyurus	Bronze Whaler	*Carcharhinidae*	Com	TL		2940	4531	0.027	–3.477	25			♂ & ♀ combined				Vertebra centrum section	Internal bands	Walter and Ebert (1991)	L
Carcharhinus obscurus	Dusky Shark	*Carcharhinidae*	Com	FL	127	2820	3544	0.043	–6.00	32	111	2620	3365	0.045	–6.00	25	Vertebra centrum section	Internal bands	Simpfendorper *et al*. (2002)	L
Sphyrna zygaena	Smooth hammerhead	*Sphyrnidae*	Com		nd						nd									
Furgaleus macki	Whiskery Shark	*Triakidae*	Com	FL	112	1300	1207	0.369	–0.544	11	67		1215	0.423	–0.544	10	Vertebra centrum section	Internal bands	Simpfendorper *et al*. (2000)	M
Galeorhinus galeus	School Shark	*Triakidae*	Abun	TL	655		1829	0.124	–1.29	42	655		♂ & ♀ combined				Whole vertebra centrum	External bands	Moulten *et al*. (1992)	L
Hypogaleus hyugaensis	Pencil Shark	*Triakidae*	Spar																	
Mustelus antarcticus	Gummy Shark (West Kangaroo I)	*Triakidae*	Abun	TL	334		2188	0.064	–4.99	15	137		1275	0.304	–0.86	13	Whole vertebra centrum	External bands	Moulten *et al*. (1992)	M
	Gummy Shark (East Kangaroo I)		Abun	TL	134	1852	2019	0.123	–1.55	16	95	1482	1387	0.253	–0.90	13	Whole vertebra centrum	External bands	Moulten *et al*. (1992)	M
Mustelus sp B	White-spotted Gummy Shark	*Triakidae*	Rare		nd						nd									

Table 3 (continued)

Scientific name	Common name	Family	Abundance	Length type	Female growth (von Bertalanffy)						Male growth (von Bertalanffy)						Tissue	Count	Growth reference	BP
					No. aged	L_{Max} (mm)	L_∞ (mm)	K (yr^{-1})	a_0 (yr)	Max age	No. aged	L_{Max} (mm)	L_∞ (mm)	K (yr^{-1})	a_0 (yr)	Max age				
Rajiformes	Skates																			
Amblyraja hyperborea	Boreal skate	*Rajidae*	Rare		nd						nd									
Dipturus australis	Sydney skate	*Rajidae*	Abun		nd						nd									
Dipturus cerva	White-spotted skate	*Rajidae*	Com	TL		658		0.138		9		620		0.159		9			Treloar (in preparation)	M
Dipturus gudgeri	Bight skate	*Rajidae*	Com	TL		1844				17		1556				18			Treloar (in preparation)	L
Dipturus lemprieri	Thornback skate	*Rajidae*	Spar		nd						nd									
Dipturus whitleyi	Melbourne skate	*Rajidae*	Abun							16						10			Treloar (in preparation)	M
Dipturus sp A	Longnose skate	*Rajidae*	Com	TL		668		0.112		11		700		0.073		12			Treloar (in preparation)	M
Dipturus sp B	Grey Skate	*Rajidae*	Spar	TL	nd	936					nd	865								
Dipturus sp J	Deepwater skate	*Rajidae*	Spar		nd						nd									
Dipturus sp M	Pigmy thornback skate	*Rajidae*	Rare		nd						nd									
Dipturus sp P	Challenger Skate	*Rajidae*	Rare		nd						nd									
Irolita waitii	Southern round skate	*Rajidae*	Rare		nd						nd									
Notoraja sp A	Blue skate	*Rajidae*	Rare		nd						nd									
Pavoraja nitida	Peacock skate	*Rajidae*	Com		nd						nd									
Myliobatiformes	Eagle & devil rays, stingrays & stingarees																			
Dasyatis brevicaudata	Smooth Stingray	*Dasyatididae*	Com		nd						nd									
Dasyatis thetidis	Black Stingray	*Dasyatididae*	Com		nd						nd									
Myliobatis australis	Southern eagle ray	*Myliobatidae*	Abun	DW		1350	1439	0.063	–3.86	32		990	880	0.209	–1.61	14	Whole vertebra centrum	External bands	David Phillips (unpublished data)	L
Trygonoptera mucosa	Western shovelnose stingaree	*Urolophidae*	Com	DW	324		308	0.241	–2.51	17	400		261	0.493	–1.36	13	Vertebra centrum section	Internal bands	White *et al.* (2002)	M
Trygonoptera testacea	Common stingaree	*Urolophidae*	Com		nd						nd									
Trygonoptera sp B	Eastern shovelnose stingaree	*Urolophidae*	Com	TL	56	760	924	0.115	–0.77	13	46	734	994	0.090	–1.75	10	Vertebra centrum section	Internal bands	Trinnie (unpublished data)	M
Urolophus bucculentus	Sandyback stingaree	*Urolophidae*	Com	TL	138	885	1112	0.062	–5.01	17	63	672	712	0.135	–4.05	11	Vertebra centrum section	Internal bands	Trinnie (unpublished data)	M
Urolophus cruciatus	Banded stingaree	*Urolophidae*	Com	TL	10	442	450	0.015	–3.00	10	11	351	id	id	id	4	Vertebra centrum section	Internal bands	Trinnie (unpublished data)	M
Urolophus expansus	Wide stingaree	*Urolophidae*	Abun		nd						nd									
Urolophus gigas	Spotted stingaree	*Urolophidae*	Spar	TL	31	800	863	0.129	–2.70	9	20	550	518	0.572	–0.79	6	Vertebra centrum section	Internal bands	Trinnie (unpublished data)	M
Urolophus kapalensis	Kapala stingaree	*Urolophidae*	Spar		nd						nd									
Urolophus ovarius	Coastal stingaree	*Urolophidae*	Spar		nd						nd									
Urolophus paucimaculatus	Sparsely-spotted stingaree	*Urolophidae*	Abun	TL	46	500	1875	0.014	–8.47	9	54	401	350	0.391	–1.62	9	Vertebra centrum section	Internal bands	Trinnie (unpublished data)	M
Urolophus sufflavus	Yellowback stingaree	*Urolophidae*	Spar		nd						nd									
Urolophus viridis	Green-backed stingaree	*Urolophidae*	Abun	TL	10	495				10		428				nd	Vertebra centrum section	Internal bands	Trinnie (unpublished data)	M
Rhinobatiformes	Shovelnose and guitar rays																			
Aptychotrema rostrata	Eastern shovelnose ray	*Rhinobatidae*	Abun		nd						nd									
Aptychotrema vincentiana	Western shovelnose ray	*Rhinobatidae*	Spar		nd						nd									
Trygonorrhina fasciata	Southern fiddler ray	*Rhinobatidae*	Abun		nd						nd									
Trygonorrhina sp A	Eastern fiddler ray	*Rhinobatidae*	Rare		nd						nd									
Torpediniformes	Electric rays																			
Hypnos monopterygium	Coffin ray	*Hypnidae*	Spar		nd						nd									
Narcine tasmaniensis	Tasmanian numbfish	*Narcinidae*	Com		nd	412					nd	365					No known ageing method		CSIRO (unpublished data)	
Torpedo macneilli	Short-tail torpedo ray	*Narcinidae*	Com		nd	1150					nd	735					No known ageing method		CSIRO (unpublished data)	
Holocephaliformes	Chimaeras																			
Callorhinchus milii	Elephant fish	*Callorhinchidae*	Abun	FL	155	885	885	0.090	–2.98	21	116	877	675	0.100	–3.13	23	First dorsal-fin spine	Inner trunk dentine layer	Bell (in preparation)	L
Chimaera lignaria	Giant chimaera	*Callorhinchidae*	Rare	FL	31	1147	1098	0.040	–6.77	43			♂ & ♀ combined				First dorsal-fin spine	Inner trunk dentine layer	Bell (in preparation)	L
Chimaera sp A	Southern chimaera	*Chimaeridae*	Spar	FL	75	825	825	0.070	–2.05	36			♂ & ♀ combined				First dorsal-fin spine	Inner trunk dentine layer	Bell (in preparation)	L
Hydrolagus lemures	Blackfin Ghostshark	*Chimaeridae*	Rare		nd	940					nd	1160								
Hydrolagus ogilbyi	Ogilbys Ghostshark	*Chimaeridae*	Spar	FL	106	750	812	0.040	–5.16	41	80	682	991	0.020	–8.94	36	First dorsal-fin spine	Inner trunk dentine layer	Bell (in preparation)	L
Hydrolagus sp A	Black ghostshark	*Chimaeridae*	Spar		nd	1100					nd	996								
Hydrolagus sp C	Giant ghostshark	*Chimaeridae*	Rare		nd						nd									
Harriotta raleighana	Bigspine spookfish	*Rhinochimaeridae*	Rare		nd						nd									
Rhinochimaera pacifica	Pacific spookfish	*Rhinochimaeridae*	Rare	FL	53	937	935	0.080	–4.96	31	40	752	721	0.180	–0.66	26	First dorsal-fin spine	Inner trunk dentine layer	Bell (in preparation)	L

[A]Common before fishing;[B]Abundant before fishing;[C]Historically H (high) when targeted.

Table 4. Biological productivity: reproduction

The table excludes those species that rarely occur in south-eastern Australia and have the main centres of their populations outside this region. RM, Reproductive mode; OP, oviphagus; OV, oviparous; AV, aplacental viviparity; PV, Placental viviparous; Mix, mix; CC, clasper calcification; SV, seminal vesicle; TD, teses development.

Table 4 (continued)

Scientific name	Common name	Family	RM	Length type	Female reproduction																	Male reproduction									Reproduction reference
					Maternity or Maturity parameter values									No. embryos–length parameter values					Parturition frequency	Litter size at L_{50}	Annual no. of embryos or eggs at L_{50}	Maturity parameter values									
					Maternity or Maturity	n	N	P_{Max}	L_{50} (mm)	L_{95} (mm)	L_{Mid} (mm)	L_{Mmin} (mm)	L_{Imax} (mm)	Equation	n	a	b	c				Method	n	N	P_{Max}	L_{50} (mm)	L_{95} (mm)	L_{Mid} (mm)	L_{Mmin} (mm)	L_{Imax} (mm)	
Pelagic and semipelagic species																															
Lamniformes	Mackerel & thresher sharks																														
Alopias vulpinus	Thresher shark	*Alopiidae*	OP											Mean		4.0				4.0											Cailliet and Beford (1983)
Isurus oxyrinchus	Shortfin mako	*Lamnidae*	OP	FL	Maturity		68	0.33	2730	2850				Power		0.810	0.002346		0.33	7.2	2.4										Mollet *et al.* (2000)
Lamna nasus	Porbeagle	*Lamnidae*	OP	FL	Maturity		284	1.00	2175	2310				Mean		4.0			1.00	4.0	4.0	Mix		267	1.00	1737	1910				Jensen *et al.* (2002)
Carcharhiniformes	Whaler & hammerhead sharks																														
Prionace glauca	Blue shark	*Carcharhinidae*	PV	TL	Maturity		26		1800													SV		204	1.00	1940					Francis and Duffy (2005)
				FL				1.00						Linear	128	0.605	–91.97		1.00	17	17										Castro and Mejuto (1995)
Myliobatiformes																															
Manta birostris	Manta ray	*Mobulidae*	AV	DW	Maturity		28				3950	4126	3774											19	1.00	3752	3800				White *et al.* (2006)
Demersal species																															
Hexanchiformes	Sixgill & sevengill sharks																														
Chlamydoselachus anguineus	Frill shark	*Chlamydoselachidae*	AV	TL	Maturity						1400			Mean		6.0				6.0								1100			Cortés (2000)
Heptranchias perlo	Sharpnose sevengill shark	*Hexanchidae*	AV	TL	Maturity		36				1045	1160	930									Mix	4	24	1.00			835	820	850	Frentzel-Beyme and Köster (2002)
Hexanchus nakamurai	Bigeye sixgill shark	*Hexanchidae*	AV			nd																									
Hexanchus griseus	Bluntnose sixgill shark	*Hexanchidae*	AV	TL	Maturity						4210			Mean		65.0				65.0								3250			Cortés (2000)
Notorynchus cepedianus	Broadnose sevengill shark	*Hexanchidae*	AV	TL	Maturity						2310			Mean		79.0				79.0								1550			Cortés (2000)
Squaliformes	Dogfishes																														
Echinorhinus brucus	Bramble shark	*Echinorhinidae*	AV	TL	Maturity						2100			Mean		20.5				20.5					1.00			1500			Kyne and Simpfendorfer (2007)
Oxynotus bruniensis	Prickly dogfish	*Echinorhinidae*	AV			nd																									
Centrophorus harrissoni	Harrissons dogfish	*Squalidae*	AV		Maturity		59				1000	980	1020	Mean	28	2.0				2.0		CC		79	1.00			820	800	840	Daley *et al.* (2002)
Centrophorus moluccensis	Endeavour dogfish	*Squalidae*	AV		Maturity		10				785	880	690	Mean	7	2.0				2.0		CC		6	1.00			715	710	520	Daley *et al.* (2002)
Centrophorus zeehani	Southern dogfish	*Squalidae*	AV		Maturity		86				990	960	1020	Mean	37	1.0				1.0		CC		74	1.00			820	810	830	Daley *et al.* (2002)
Centroscyllium kamoharai	Bareskin dogfish	*Squalidae*	AV		Maturity		164				550	530	570	Mean	16	12.0						CC		70	1.00			440	440	440	Daley *et al.* (2002)
Centroscymnus crepidater	Golden dogfish	*Squalidae*	AV	TL	Maturity		238	1.00	840	900				Mean		6.0				6.0		CC		155	1.00	640	680				Irvine (2004)
Centroscymnus coelolepis	Portugese dogfish	*Squalidae*	AV	TL	Maturity		29	1.00	990	1040												CC		72	1.00	820	840				Irvine (2004)
Centroscymnus owstoni	Owstons dogfish	*Squalidae*	AV	TL	Maturity		41	1.00	990	1010												CC		30	1.00	700	nd				Irvine (2004)
Centroscymnus plunketi	Plunkets dogfish	*Squalidae*	AV	TL	Maturity		37	1.00	1320	1360				Mean		17.0				17.0		CC		29	1.00	1120	nd				Irvine (2004)
Cirrhigaleus barbifer	Mandarin shark	*Squalidae*	AV	TL	Maturity						1140			Mean		8.0				8.0								925			Kyne and Simpfendorfer (2007)
Dalatias licha	Black shark	*Squalidae*	AV		Maturity		42	1.00			1205	1270	1140	Mean	4	9.0				9.0		CC		27					1130	1090	Daley *et al.* (2002)
Deania calcea	Brier shark	*Squalidae*	AV	TL	Maturity		43	1.00	970	1040				Mean		8.0				8.0		CC		47	1.00	760	780				Irvine (2004)
Deania quadrispinosa	Longsnout dogfish	*Squalidae*	AV		Maturity		64	1.00			915	1020	810	Mean	1	8.0				8.0		CC		95	1.00			815	800	830	Daley *et al.* (2002)
Etmopterus baxteri	Giant lantern shark	*Squalidae*	AV	TL	Maturity		641	1.00	630	680				Linear		–15.2	0.035			6.8		CC		366	1.00	540	580				Irvine (2004)
Etmopterus bigelowi	Smooth lantern shark	*Squalidae*	AV			nd																									
Etmopterus granulosus	Southern lantern shark	*Squalidae*	AV		Maturity		714	1.00			645	600	690	Mean	19	10.0				10.0		CC		286	1.00			645	600	690	Daley *et al.* (2002)
Etmopterus lucifer	Blackbelly lantern shark	*Squalidae*	AV			nd																									
Etmopterus pusillus	Slender Lantern shark	*Squalidae*	AV	TL	Maturity			0.50			445	419	470	Mean	3.5				0.50	3.5	1.75	Mix						386	354	417	Coelho and Erzini (2007)
Etmopterus sp B	Bristled latern shark	*Squalidae*	AV	TL	Maturity		253	1.00			620	570	670	Mean	24	12.0				12.0		CC		159	1.00			510	500	520	Daley *et al.* (2002)
Isistius brasiliensis	Cookie-cutter shark	*Squalidae*	AV			nd																									
Somniosus pacificus	Pacific sleeper shark	*Squalidae*	AV	TL	Maturity						3700																				Kyne and Simpfendorfer (2007)
Squalus acanthias	White-spotted spurdog	*Squalidae*	AV	TL	Maturity		2463	0.50	740	810				Linear	256	0.209	6.128		0.50	22	11	CC		1338	1.00	575	610				Hanchet (1988)
Squalus chloroculus	Green-eyed spurdog	*Squalidae*	AV		Maturity		106	1.00			810	800	820	Mean	7	7.0						CC		93	1.00			650	630	670	Daley *et al.* (2002)
Squalus megalops	Spikey spurdog	*Squalidae*	AV	TL	Maternity		522	0.50	531	626				Linear		–1.5	0.00711		0.50	2.3	1.1	CC		201	1.00	393	417				Braccini *et al.* (2006)
Zameus squamulosus	Velvet dogfish	*Squalidae*	AV			nd																									

Table 4 (continued)

Scientific name	Common name	Family	RM	Length type	Female reproduction																	Male reproduction									Reproduction reference
					Maternity or Maturity parameter values									No. embryos–length parameter values					Parturition frequency	Litter size at L_{50}	Annual no. of embryos or eggs at L_{50}	Maturity parameter values									
					Maternity or Maturity	n	N	P_{Max}	L_{50} (mm)	L_{95} (mm)	L_{Mid} (mm)	L_{Mmin} (mm)	L_{Imax} (mm)	Equation	n	a	b	c				Method	n	N	P_{Max}	L_{50} (mm)	L_{95} (mm)	L_{Mid} (mm)	L_{Mmin} (mm)	L_{Imax} (mm)	
Pristiophoriformes	Sawsharks																														
Pristiophorus cirratus	Common sawshark	*Pristiophoridae*	AV	TL	Maternity		1049	0.50	1156	1239				Linear		–14.5	0.0205		0.50	9.198	4.6										Hudson *et al.* (2005)
Pristiophorus nudipinnis	Southern sawshark	*Pristiophoridae*	AV	TL	Maternity		416	0.50	944	954				Linear		–8.4	0.0184		0.50	9.0	4.5										Walker and Hudson (2005)
Pristiophorus sp A	Eastern sawshark	*Pristiophoridae*	AV																												
Squatiniformes	Angel sharks																														
Squatina australis	Australian angel shark	*Squatinidae*	AV	TL	Maternity	15	151				759	795	723																		
Squatina tergocellata	Ornate angel shark	*Squatinidae*	AV	TL	Maturity		128	0.50			1200			Mean		4.5			0.5	4.5	2.25	CC		56	1.00			925	880	970	Bridge *et al.* (1998)
Squatina sp A	Eastern angel shark	*Squatinidae*	AV			nd																									
Heterodontiformes	Horn sharks					nd																									
Heterodontus galeatus	Crested horn shark	*Heterodontidae*	OV																												
Heterodontus portusjacksoni	Port Jackson shark (west Victoria)	*Heterodontidae*	OV	TL	Maturity	9	77	1.00	858	1021									1.00			SV	29	68	1.00	678	793				Tovar-Ávila *et al.* (2007)
	Port Jackson shark (east Victoria)	*Heterodontidae*	OV	TL	Maturity	106	208	1.00	990	1178									1.00			SV	157	226	1.00	815	905				Tovar-Ávila *et al.* (2007)
Orectolobiformes	Catsharks, wobbegongs, carpet																														
Brachaelurus waddi	Blind Shark	*Brachaeluridae*	AV			nd																									
Orectolobus halei	Ornate wobbegong	*Orectolobidae*	AV	TL	Maternity	64	161	0.33	1743	1902									0.33			CC	51	146	1.00	1784	1938				Huveneers *et al.* (2007)
Orectolobus maculatus	Spotted wobbegong	*Orectolobidae*	AV	TL	Maternity	14	65	0.33	1281	1546				Linear	13	–1.8	0.017		0.33	20.0	6.6	CC	59	96	1.00	1282	1360				Huveneers *et al.* (2007)
Orectolobus ornatus	Dwarf wobbegong	*Orectolobidae*	AV	TL	Maternity	50	147	0.33	805	901				Linear	42	–20.9	0.034		0.33	6.5	2.1	CC	143	182	1.00	803	867				Huveneers *et al.* (2007)
Sutorectus tentaculatus	Cobbler wobbegong	*Orectolobidae*	AV			nd																									
Parascyllium collare	Collared carpet shark	*Parascylliidae*	OV			nd																									
Parascyllium ferrugineum	Rusty carpet shark	*Parascylliidae*	OV	TL	Maturity	38	47	1.00	617	701				nd					1.00			CC	28	30	1.00	483	596				Mossop (2004)
Parascyllium variolatum	Varied carpet shark	*Parascylliidae*	OV			nd																									
Apristurus sp A	Freckled catshark	*Scyliorhinidae*	OV			nd																									
Apristurus sp C	Fleshynose catshark	*Scyliorhinidae*	OV			nd																									
Apristurus sp D	Roughskin catshark	*Scyliorhinidae*	OV			nd																									
Apristurus sp E	Bulldog catshark	*Scyliorhinidae*	OV			nd																									
Apristurus sp G	Pinocchio catshark	*Scyliorhinidae*	OV			nd																									
Asymbolus analis	Grey spotted catshark	*Scyliorhinidae*	OV			nd																									
Asymbolus occiduus	Western spotted catshark	*Scyliorhinidae*	OV			nd																									
Asymbolus rubiginosus	Orange spotted catshark	*Scyliorhinidae*	OV	TL	Maturity	197	221	1.00	359	396				nd								CC	169	192	1.00	360	411				Mossop (2004)
Asymbolus vincenti	Gulf catshark	*Scyliorhinidae*	OV			nd																									
Cephaloscyllium laticeps	Draughtboard shark	*Scyliorhinidae*	OV	TL	Maturity		609	1.00	815	873												CC		462	1.00	761	815				Awruch (2007)
Cephaloscyllium sp A	Whitefinned swell shark	*Scyliorhinidae*	OV			nd																									
Galeus boardmani	Sawtail shark	*Scyliorhinidae*	OV			nd																									
Lamniformes	Mackerel & thresher sharks																														
Carcharidon carcharias	White shark	*Lamnidae*	OP	TL	Maturity			0.33			4570			Mean		9.5			0.33	9.5	3.14							4260			Bruce (2008)
Mitsukurina owstoni	Goblin shark	*Mitsukurinidae*	OP			nd																									
Carcharias taurus	Grey nurse shark	*Odontaspididae*	OP	TL	Maturity		77	0.50			2265	2350	2180	Mean		2.0			0.50	2.0	1.0	Mix		162	1.00			1890	1930	1850	Lucifora *et al.* (2002)
Odontaspis ferox	Smalltooth sandtiger shark	*Odontaspididae*	OP	TL	Maturity						3150	3500	2800									CC		11	1.00			1840	2000	1680	Fergusson *et al.* (2008)
Carcharhiniformes	Whaler & hammerhead sharks																														
Carcharhinus brachyurus	Bronze Whaler	*Carcharhinidae*	AV	TL	Maturity		207		2221					Mean		16.0				16.0		CC		96	1.00	2162	2300				Lucifora *et al.* (2005)
Carcharhinus obscurus	Dusky Shark	*Carcharhinidae*	AV	TL	Maturity			0.50			2800			Mean		9.9			0.50	9.9	4.95							2800			Cortés (2000)
Sphyrna zygaena	Smooth hammerhead	*Sphyrnidae*	AV	TL	Maturity						2250			Mean		33.0												2250			Cortés (2000)
Furgaleus macki	Whiskery Shark	*Triakidae*	AV	TL	Maturity		583	0.50	1112					Linear		0.314	–17.8		0.50	17.0	8.5	SV		302	1.00	1070					Simpfendorfer and Unsworth (1998)
Galeorhinus galeus	School Shark	*Triakidae*	AV	TL	Maternity	53	269	0.33	1421	1488				Linear		–46.0	0.0491		0.33	23.77	7.9	SV	223	585	1.00	1260	1415				Walker (2005)
Hypogaleus hyugaensis	Pencil Shark	*Triakidae*	PV	TL	Maturity		260	0.50			860			Mean		8.5			0.50	8.5	4.25	CC		254	1.00			820			Simpfendorfer *et al.* (2002c)
Mustelus antarcticus	Gummy Shark (West Kangaroo I)	*Triakidae*	AV	TL	Maternity	49	129	1.00	1263	1523				Exp.	57	–3.03	0.00396	1.12	1.00	8.0	8.0	SV	188	364	1.00	953	1245				Walker (2007)
	Gummy Shark (East Kangaroo I)		AV	TL	Maternity	39	274	0.50	1129	1344				Exp.	80	–1.38	0.00286	1.10	0.50	7.0	3.5	SV	89	106	1.00	978	1119				Walker (2007)
Mustelus sp B	White-spotted Gummy Shark	*Triakidae*				nd																									

Table 4 (continued)

					Female reproduction																	Male reproduction									Reproduction reference
					Maternity or Maturity parameter values									No. embryos–length parameter values								Maturity parameter values									
Scientific name	Common name	Family	RM	Length type	Maternity or Maturity	n	N	P_{Max}	L_{50} (mm)	L_{95} (mm)	L_{Mid} (mm)	L_{Mmin} (mm)	L_{Imax} (mm)	Equation	n	a	b	c	Parturition frequency	Litter size at L_{50}	Annual no. of embryos or eggs at L_{50}	Method	n	N	P_{Max}	L_{50} (mm)	L_{95} (mm)	L_{Mid} (mm)	L_{Mmin} (mm)	L_{Imax} (mm)	
Rajiformes	Skates																														
Amblyraja hyperborea	Boreal skate	*Rajidae*	OV			nd																									
Dipturus australis	Sydney skate	*Rajidae*	OV			nd																									
Dipturus cerva	White-spotted skate	*Rajidae*	OV		Maturity			1.00	487			470													1.00	470			457		Treloar (in preparation)
Dipturus gudgeri	Bight skate	*Rajidae*	OV		Maturity			1.00				1676													1.00				1221		Treloar (in preparation)
Dipturus lemprieri	Thornback skate	*Rajidae*	OV			nd																									
Dipturus whitleyi	Melbourne skate	*Rajidae*	OV			nd																									
Dipturus sp A	Longnose skate	*Rajidae*	OV		Maturity			1.00	530			525													1.00	480			470		Treloar (in preparation)
Dipturus sp B	Grey Skate	*Rajidae*	OV		Maturity			1.00	844			765													1.00	713			715		Treloar (in preparation)
Dipturus sp J	Deepwater skate	*Rajidae*	OV			nd																									
Dipturus sp M	Pigmy thornback skate	*Rajidae*	OV			nd																									
Dipturus sp P	Challenger Skate	*Rajidae*	OV			nd																									
Irolita waitii	Southern round skate	*Rajidae*	OV			nd																									
Notoraja sp A	Blue skate	*Rajidae*	OV			nd																									
Pavoraja nitida	Peacock skate	*Rajidae*	OV			nd																									
Myliobatiformes	Eagle & devil rays and stingrays																														
Dasyatis brevicaudata	Smooth Stingray	*Dasyatididae*	AV			nd																									
Dasyatis thetidis	Black Stingray	*Dasyatididae*	AV			nd																									
Myliobatis australis	Southern eagle ray	*Myliobatidae*	AV	DW	Maturity		251	1.00	769	1175												CC		197	1.00	721	856				Phillips (in preparation)
Trygonoptera mucosa	Western shovelnose stingaree	*Urolophidae*	AV	TL	Maturity			1.00	253					Mean		1.2			1.00	1.2	1.2	TD			1.00	222					White *et al.* (2002)
Trygonoptera sp B	Eastern shovelnose stingaree	*Urolophidae*	AV	TL	Maternity	188	294	1.00	563	665				Linear	24	−11.25	0.02200		1.00	1.1	1.1	SV	103	279	1.00	481	548				Trinnie (in preparation)
Trygonoptera testacea	Common stingaree	*Urolophidae*	AV			nd																									
Urolophus bucculentus	Sandyback stingaree	*Urolophidae*	AV	TL	Maternity	26	125	0.50	632	715				Linear	19	−1.77	0.00567		0.50	1.8	0.9	CC	58	77	1.00	411	446				Trinnie (in preparation)
Urolophus cruciatus	Banded stingaree	*Urolophidae*	AV	TL	Maturity	401	420	0.50	193	239				Linear	22	−3.84	0.01900		0.50	-0.2	-0.1	SV	282	307	1.00	212	253				Trinnie (in preparation)
Urolophus expansus	Wide stingaree	*Urolophidae*	AV			nd																									
Urolophus kapalensis	Kapala stingaree	*Urolophidae*	AV			nd																									
Urolophus gigas	Spotted stingaree	*Urolophidae*	AV	TL	Maturity	18	48	1.00	457	539				Mean	6	5.0			1.00	5.0	5.0	SV	49	68	1.00	397	430				Trinnie (in preparation)
Urolophus ovarius	Coastal stingaree	*Urolophidae*	AV			nd																									
Urolophus paucimaculatus	Sparsely-spotted stingaree	*Urolophidae*	AV	TL	Maternity	116	682	1.00	351	511				Linear	130	−3.17	0.01500		1.00	2.095	2.1	SV	473	597	1.00	268	301				Trinnie (in preparation)
Urolophus sufflavus	Yellowback stingaree	*Urolophidae*	AV			nd																									
Urolophus viridis	Green-backed stingaree	*Urolophidae*	AV	TL	Maturity	192	207	1.00	279	317				Linear	58	−1.01	0.00600		1.00	0.7	0.7	SV	99	104	1.00	386	308				Trinnie (in preparation)
Rhinobatiformes	Shovelnose and guitar rays																														
Aptychotrema rostrata	Eastern shovelnose ray	*Rhinobatidae*	AV	TL	Maturity	41	48	1.00			600			Linear	48	0.529	−29.153		1.00	8.0	8.0	TD	33	53	1.00			640			Kyne and Bennett (2002)
Aptychotrema vincentiana	Western shovelnose ray	*Rhinobatidae*	AV			nd																									
Trygonorrhina fasciata	Southern fiddler ray	*Rhinobatidae*	AV	TL					892					Linear	12	−8.8	0.012		1.00	1.9	1.9	TD			1.00	678					
Trygonorrhina sp A	Eastern fiddler ray	*Rhinobatidae*	AV			nd																									
Torpediniformes	Electric rays																														
Hypnos monopterygium	Coffin ray	*Hypnidae*	AV			nd																									
Narcine tasmaniensis	Tasmanian numbfish	*Narcinidae*	AV			nd																									
Torpedo macneilli	Short-tail torpedo ray	*Narcinidae*	AV			nd																									
Holocephaliformes	Chimaeras																														
Callorhinchus milii	Elephant fish	*Callorhinchidae*	OV	TL	Maternity	635	836	1.00	659	888				Linear	7	19.5	0		1.00	19.5	19.5	CI	696		1.00	560					Bell (in preparation)
Chimaera lignaria	Giant chimaera	*Chimaeridae*	OV	PL	Maturity	54			780													CI	65		1.00	600					Bell (in preparation)
Chimaera sp A	Southern chimaera	*Chimaeridae*	OV	PL	Maturity	111			650													CI	88		1.00	580					Bell (in preparation)
Hydrolagus sp C	Giant ghostshark	*Chimaeridae*	OV	PL		nd																									
Hydrolagus lemures	Blackfin Ghostshark	*Chimaeridae*	OV	PL	Maturity	54			560																						Bell (in preparation)
Hydrolagus ogilbyi	Ogilbys Ghostshark	*Chimaeridae*	OV	PL	Maturity	203			635													CI	143		1.00	530					Bell (in preparation)
Hydrolagus sp A	Black ghostshark	*Chimaeridae*	OV	PL	Maturity	25			700													CI	54		1.00	590					Bell (in preparation)
Harriotta raleighana	Bigspine spookfish	*Rhinochimaeridae*	OV			nd																									
Rhinochimaera pacifica	Pacific spookfish	*Rhinochimaeridae*	OV	PL	Maturity	110			830													CI	88		1.00	690					Bell (in preparation)

[A]Common before fishing;[B]Abundant before fishing;[C]Historically H (high) when targeted.

Table 5. Catch susceptibility of chondrichthyan animals to demersal fishing gear in the South East Scalefish and Shark Fishery

Catch susceptibility relates to the proportion of a population dying from one unit of fishing effort and is defined as 'availability' x 'encounterability' x 'selectivity' x 'post-capture mortality'; 'availability' is the ratio of the area of the range of the fishery impacting a species divided by the area of the distributional range of the species; ‘encounterability’ is the proportion of that part of the population available to the fishery encountering the gear; selectivity’ is the proportion of the animals encountering the fishing gear that is captured; post-capture mortality’ is the proportion of the animals that die as a result of capture by the gear the fishing gear; 'catch susceptibility', 'availability', 'encounterability', 'selectivity', and 'discard post-harvest mortality' all have values ranging 0–1 and for risk assessment these are categorised as L (low, 0.00–0.33), M (medium, 0.34–0.66), and H (high, 0.67–1.00); Y, yes; N, no; R, rarely. The table excludes those species that rarely occur in south-eastern Australia and have the main centres of their populations outside this region.

Table 5 (continued)

Scientific name	Common name	Family	Distribution				Depth stratum	Abundance (present)	Mean annual catch (t) 2000– 06 ISMP estimate	Availability					Encounterability					Selectivity					Post-capture mortality					Catch susceptibility				
			SA	BS	Tas	NSW				Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot
Pelagic and semipelagic species																																		
Lamniformes	Mackerel & thresher sharks																																	
Alopias vulpinus	Thresher shark	*Alopiidae*	Y	Y	Y	Y	Shelf, oceanic	Common	16	L	L	L	L	L	L	M	M	M	L	H	M	H	H	L	H	H	M	M	H	L	L	L	L	L
Isurus oxyrinchus	Shortfin mako	*Lamnidae*	Y	Y	Y	Y	Shelf, oceanic	Common	2	L	L	L	L	L	L	L	M	M	L	H	M	H	H	L	H	H	M	M	H	L	L	L	L	L
Lamna nasus	Porbeagle	*Lamnidae*	Y	Y	Y	Y	Shelf, oceanic	Rare	<1	L	L	L	L	L	L	L	M	M	L	H	M	H	H	L	H	H	M	M	H	L	L	L	L	L
Carcharhiniformes	Whaler & hammerhead sharks																																	
Prionace glauca	Blue shark	*Carcharhinidae*	Y	Y	Y	Y	Shelf, oceanic	Abundant	<1	L	L	L	L	L	L	L	L	L	L	H	H	H	H	L	H	H	M	M	H	L	L	L	L	L
Myliobatiformes																																		
Manta birostris	Manta ray	*Mobulidae*	N	N	N	Y	Shelf, oceanic	Common	nd	L	L	L	L	L	L	L	L	L	L	H	L	H	H	L	H	M	M	M	M	L	L	L	L	L
Demersal species																																		
Hexanchiformes	Sixgill & sevengill sharks																																	
Chlamydoselachus anguineus	Frill shark	*Chlamydoselachidae*	N	Y	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	M	H	H	H	L	H	L	H	H	L	H	H	M	M	H	M	L	L	L	L
Heptranchias perlo	Sharpnose sevengill shark	*Hexanchidae*	Y	Y	Y	Y	Upper slope	Sparse	19	H	L	L	H	L	M	H	H	H	L	H	H	H	H	L	H	H	H	H	H	M	L	L	H	L
Hexanchus nakamurai	Bigeye sixgill shark	*Hexanchidae*	N	N	N	Y	Mid-slope	Rare	nd	H	L	L	H	L	M	H	H	H	L	H	M	H	H	L	H	H	M	M	H	M	L	L	M	L
Hexanchus griseus	Bluntnose sixgill shark	*Hexanchidae*	N	Y	Y	Y	Entire slope	Rare	<1	H	L	L	L	L	M	H	H	H	L	H	M	H	H	L	H	H	M	M	H	M	L	L	L	L
Notorynchus cepedianus	Broadnose sevengill shark	*Hexanchidae*	Y	Y	Y	Y	Shelf	Common	3	L	H	L	L	L	M	H	H	H	L	H	M	H	H	L	H	H	H	H	H	L	M	L	L	L
Squaliformes	Dogfishes																																	
Echinorhinus brucus	Bramble shark	*Echinorhinidae*	Y	Y	N	N	Mid-slope	Rare	nd	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Oxynotus bruniensis	Prickly dogfish	*Echinorhinidae*	Y	Y	N	N	Upper slope	Sparse	1	H	L	L	L	L	H	H	H	H	L	H	H	H	H	M	H	H	H	H	M	H	L	L	L	L
Centrophorus harrissoni	Harrissons dogfish	*Squalidae*	N	Y	N	Y	Upper slope	Rare	<1	H	L[C]	L[C]	H	L	H	H	H	H	L	H	H	H	H	M	H	H	H	H	M	H	L	L	H	L
Centrophorus moluccensis	Endeavour dogfish	*Squalidae*	N	Y	N	Y	Upper slope	Common	30	H	L[C]	L[C]	H	L	H	H	H	H	L	H	H	H	H	M	H	H	H	H	M	H	L	L	H	L
Centrophorus zeehani	Southern dogfish	*Squalidae*	Y	Y	Y	Y	Upper slope	Sparse	12	H	L[C]	L[C]	H	L	H	H	H	H	L	H	H	H	H	M	H	H	H	H	M	H	L	L	H	L
Centroscyllium kamoharai	Bareskin dogfish	*Squalidae*	N	N	N	Y	Mid-slope	Rare	<1	H	L[C]	L[C]	H	L	H	H	H	H	L	H	H	H	H	M	H	H	H	H	M	H	L	L	H	L
Centroscymnus crepidater	Golden dogfish	*Squalidae*	Y	Y	Y	Y	Mid-slope	Common	56	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Centroscymnus coelolepsis	Portugese dogfish	*Squalidae*	Y	Y	Y	Y	Mid-slope	Sparse	1	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Centroscymnus owstoni	Owstons dogfish	*Squalidae*	Y	Y	Y	Y	Mid-slope	Common	71	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Centroscymnus plunketi	Plunkets dogfish	*Squalidae*	N	Y	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Cirrhigaleus barbifer	Mandarin shark	*Squalidae*	N	N	N	Y	Mid-slope	Rare	<1	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Dalatias licha	Black shark	*Squalidae*	Y	Y	Y	Y	Mid-slope	Common	81	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Deania calcea	Brier shark	*Squalidae*	Y	Y	Y	Y	Mid-slope	Abundant	257	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Deania quadrispinosa	Longsnout dogfish	*Squalidae*	Y	Y	Y	Y	Upper slope	Sparse	4	H	L	L	L	L	H	H	H	H	L	H	H	H	H	M	H	H	H	H	M	H	L	L	L	L
Etmopterus baxteri	Giant lantern shark	*Squalidae*	N	Y	Y	Y	Mid-slope	Rare	nd	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Etmopterus bigelowi	Smooth lantern shark	*Squalidae*	N	N	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Etmopterus granulosus	Southern lantern shark	*Squalidae*	N	Y	Y	Y	Mid-slope	Sparse	15	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Etmopterus lucifer	Blackbelly lantern shark	*Squalidae*	N	N	N	Y	Mid-slope	Sparse	5	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Etmopterus pusillus	Slender lantern shark	*Squalidae*	N	Y	Y	Y	Mid-slope	Sparse	4	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Etmopterus sp B	Bristled latern shark	*Squalidae*	Y	Y	Y	Y	Lower slope	Rare	nd																									
Isistius brasiliensis	Smalltooth cookie-cutter shark	*Squalidae*	N	Y	Y	Y	Lower slope	Rare	<1	M	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Somniosus pacificus	Pacific sleeper shark	*Squalidae*	N	N	Y	N	Mid-slope	Rare	2	H	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L
Squalus acanthias	White-spotted spurdog	*Squalidae*	N	Y	Y	N	Shelf	Sparse	4	L	L	L	L	L	H	H	H	H	L	H	L	H	H	M	H	M	L	L	L	L	L	L	L	L
Squalus chloroculus	Green-eyed spurdog	*Squalidae*	Y	Y	Y	Y	Upper slope	Abundant	212	H	L[A]	L[A]	H	L	H	H	H	H	L	H	M	H	H	M	H	H	H	H	M	H	L	L	H	L
Squalus megalops	Spikey spurdog	*Squalidae*	Y	Y	Y	Y	Shelf	Abundant	719	L	H	L	L	L	H	H	H	H	L	H	L	H	H	M	H	M	L	L	L	L	L	L	L	L
Zameus squamulosus	Velvet dogfish	*Squalidae*	N	Y	Y	Y	Lower slope	Rare	<1	M	L	L	L	L	M	H	H	H	L	H	H	H	H	M	H	H	H	H	M	M	L	L	L	L

Table 5 (continued)

Scientific name	Common name	Family	Distribution				Depth stratum	Abundance (present)	Mean annual catch (t) 2000– 06 ISMP estimate	Availability					Encounterability					Selectivity					Post-capture mortality					Catch susceptibility				
			SA	BS	Tas	NSW				Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot
Pristiophoriformes	Sawsharks																																	
Pristiophorus cirratus	Common sawshark	*Pristiophoridae*	Y	Y	Y	N	Shelf	Abundant	276	L	H	L	L	L	M	H	M	M	L	H	H	H	H	M	H	H	H	H	H	L	H	L	L	L
Pristiophorus nudipinnis	Southern sawshark	*Pristiophoridae*	Y	Y	Y	N	Shelf	Common	32	L	H	L	L	L	M	H	M	M	L	H	M	H	H	M	H	H	H	H	H	L	M	L	L	L
Pristiophorus sp A	Eastern sawshark	*Pristiophoridae*	N	N	N	Y	Shelf	Sparse	nd	H	L	L	L	L	M	H	M	M	L	H	H	H	H	M	H	H	H	H	H	M	L	L	L	L
Squatiniformes	Angel sharks																																	
Squatina australis	Australian angel shark	*Squatinidae*	Y	Y	Y	Y	Shelf	Abundant	311	L	H	L	L	L	H	L	L	L	L	H	L	H	H	M	H	H	H	H	H	L	L	L	L	L
Squatina tergocellata	Ornate angel shark	*Squatinidae*	Y	N	N	N	Shelf	Abundant	289	M	H	L	L	L	H	L	L	L	L	H	L	H	H	M	H	H	H	H	H	M	L	L	L	L
Squatina sp A	Eastern angel shark	*Squatinidae*	N	R	N	Y	Shelf	Sparse	nd	H	L	M	L	L	H	L	L	L	L	H	L	H	H	M	H	H	H	H	H	H	L	L	L	L
Heterodontiformes	Horn sharks																																	
Heterodontus galeatus	Crested horn shark	*Heterodontidae*	N	N	N	Y	Shelf	Rare	<1	M	L	L	L	L	M	H	M	H	L	H	M	H	H	H	L	L	L	L	L	L	L	L	L	L
Heterodontus portusjacksoni	Port Jackson shark	*Heterodontidae*	Y	Y	Y	Y	Shelf	Abundant	211	L	H	L	L	L	M	H	M	H	L	H	M	H	H	H	L	L	L	L	L	L	L	L	L	L
Orectolobiformes	Catsharks, wobbegongs, carpet																																	
Brachaelurus waddi	Blind Shark	*Brachaeluridae*	N	N	N	Y	Shelf	Rare	<1	L	M	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Orectolobus halei	Ornate wobbegong	*Orectolobidae*	Y	Y	N	Y	Shelf	Abundant	nd	L	L	L	L	L	M	H	H	H	M	H	L	H	H	L	M	L	M	L	L	L	L	L	L	L
Orectolobus maculatus	Spotted wobbegong	*Orectolobidae*	Y	Y	N	Y	Shelf	Abundant	24	L	L	L	L	L	M	H	H	H	M	H	L	H	H	L	M	L	M	L	L	L	L	L	L	L
Orectolobus ornatus	Dwarf wobbegong	*Orectolobidae*	N	N	N	Y	Shelf	Common	<1	L	L	L	L	L	M	H	H	H	M	H	L	H	H	L	M	L	M	L	L	M	L	M	L	L
Sutorectus tentaculatus	Cobbler wobbegong	*Orectolobidae*	Y	N	N	N	Shelf	Rare	nd	L	M	L	L	L	M	H	H	H	M	H	L	H	H	L	M	L	M	L	L	L	L	L	L	L
Parascyllium collare	Collared carpet shark	*Parascylliidae*	N	Y	N	Y	Shelf	Common	10	L	M	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Parascyllium ferrugineum	Rusty carpet shark	*Parascylliidae*	Y	Y	Y	N	Shelf	Common	19	L	M	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Parascyllium variolatum	Varied carpet shark	*Parascylliidae*	Y	Y	Y	N	Shelf	Common	nd	L	M	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Apristurus sp A	Freckled catshark	*Scyliorhinidae*	Y	Y	Y	Y	Mid-slope	Rare	nd	H	L	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	M	L	L	L	L
Apristurus sp C	Fleshynose catshark	*Scyliorhinidae*	Y	Y	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	M	L	L	L	L
Apristurus sp D	Roughskin catshark	*Scyliorhinidae*	Y	N	Y	N	Mid-slope	Rare	nd	H	L	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	M	L	L	L	L
Apristurus sp E	Bulldog catshark	*Scyliorhinidae*	N	Y	Y	Y	Lower slope	Rare	nd	L	L	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Apristurus sp G	Pinocchio catshark	*Scyliorhinidae*	Y	Y	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	M	L	L	L	L
Asymbolus analis	Grey spotted catshark	*Scyliorhinidae*	N	N	N	Y	Shelf	Common	26	L	M	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Asymbolus occiduus	Western spotted catshark	*Scyliorhinidae*	Y	N	N	N	Shelf	Rare	<1	L	M	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Asymbolus rubiginosus	Orange spotted catshark	*Scyliorhinidae*	N	Y	Y	Y	Shelf	Rare	<1	L	M	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Asymbolus vincenti	Gulf catshark	*Scyliorhinidae*	Y	Y	Y	?	Shelf	Rare	<1	L	H	L	L	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	L	L	L	L	L
Cephaloscyllium laticeps	Draughtboard shark	*Scyliorhinidae*	Y	Y	Y	Y	Shelf	Abundant	227	L	H	L	L	L	M	H	H	H	M	H	H	H	H	H	M	L	L	L	L	L	L	L	L	L
Cephaloscyllium sp A	Whitefinned swell shark	*Scyliorhinidae*	Y	Y	Y	Y	Upper slope	Abundant	385	H	L	L	H	L	M	H	H	H	M	H	H	H	H	H	M	L	L	L	L	M	L	L	L	L
Galeus boardmani	Sawtail shark	*Scyliorhinidae*	Y	Y	Y	Y	Upper slope	Common	23	H	L	L	H	L	M	H	H	H	M	H	L	H	H	H	M	L	L	L	L	M	L	L	L	L
Lamniformes	Mackerel & thresher sharks																																	
Carcharidon carcharias	White shark	*Lamnidae*	Y	Y	Y	Y	Shelf	Sparse	2	L	M	L	L	L	L	H	M	M	L	H	M	H	H	L	H	H	M	M	H	L	M	L	L	L
Carcharias taurus	Grey nurse shark	*Odontaspididae*	Y	Y	N	Y	Shelf	Rare	3	L	L	L	L	L	M	H	H	H	L	H	M	H	H	L	H	H	M	M	H	L	L	L	L	L
Odontaspis ferox	Smalltooth sandtiger shark	*Odontaspididae*	N	N	N	Y	Shelf	Sparse	4	M	L	L	L	L	M	H	H	H	L	H	M	H	H	L	H	H	M	M	H	M	L	L	L	L
Mitsukurina owstoni	Goblin shark	*Mitsukurinidae*	Y	Y	N	Y	Mid-slope	Rare	nd	M	L	L	L	L	M	H	H	H	L	H	M	H	H	L	H	H	M	M	H	M	L	L	L	L
Carcharhiniformes	Whaler & hammerhead sharks																																	
Carcharhinus brachyurus	Bronze whaler	*Carcharhinidae*	Y	Y	N	Y	Shelf	Common	17	L	M	L	L	L	L	H	H	H	L	H	M	H	H	L	H	H	H	H	H	L	M	L	L	L
Carcharhinus obscurus	Dusky shark	*Carcharhinidae*	Y	Y	Y	Y	Shelf	Common	nd	L	H	L	L	L	L	H	H	H	L	H	M	H	H	L	H	H	H	H	H	L	M	L	L	L
Sphyrna zygaena	Smooth hammerhead	*Sphyrnidae*	Y	Y	Y	Y	Shelf	Common	3	L	M	L	L	L	L	H	M	H	L	H	M	H	H	L	H	H	H	H	H	L	M	L	L	L
Furgaleus macki	Whiskery shark	*Triakidae*	Y	R	R	N	Shelf	Common[B]	<1	L	H	L	L	L	L	H	M	H	L	H	H	H	H	M	H	H	H	H	H	L	H	L	L	L
Galeorhinus galeus	School shark	*Triakidae*	Y	Y	Y	Y	Shelf	Abundant	35	L	H	L	M	L	L	H	H	H	L	H	H	H	H	L	H	H	H	H	H	L	H	L	M	L
Hypogaleus hyugaensis	Pencil shark	*Triakidae*	Y	R	R	R	Shelf	Sparse	nd	L	H	L	L	L	L	H	M	H	L	H	M	H	H	M	H	H	H	H	H	L	M	L	L	L
Mustelus antarcticus	Gummy shark	*Triakidae*	Y	Y	Y	Y	Shelf	Abundant	186	L	H	L	L	L	L	H	M	H	L	H	H	H	H	M	H	H	H	H	H	L	H	L	L	L
Mustelus sp B	White-spotted gummy shark	*Triakidae*	N	N	N	Y	Shelf	Rare	<1	L	L	L	L	L	L	H	M	H	L	H	H	H	H	M	H	H	H	H	H	L	L	L	L	L

Table 5 (continued)

Scientific name	Common name	Family	Distribution				Depth stratum	Abundance (present)	Mean annual catch (t) 2000– 06 ISMP estimate	Availability					Encounterability					Selectivity					Post-capture mortality					Catch susceptibility				
			SA	BS	Tas	NSW				Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot
Rajiformes	Skates																																	
Amblyraja hyperborea	Boreal skate	*Rajidae*	?	Y	Y	N	Shelf	Rare	<1	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Dipturus australis	Sydney skate	*Rajidae*	N	N	N	Y	Shelf	Abundant	157	M	L	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	M	L	L	L	L
Dipturus cerva	White-spotted skate	*Rajidae*	Y	Y	Y	Y	Shelf	Common	37	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Dipturus gudgeri	Bight skate	*Rajidae*	Y	Y	Y	Y	Upper slope	Common	88	H	L	L	H	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	M	L	L	L	L
Dipturus lemprieri	Thornback skate	*Rajidae*	N	Y	Y	Y	Shelf	Sparse	19	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Dipturus whitleyi	Melbourne skate	*Rajidae*	Y	Y	Y	Y	Shelf	Abundant	176	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	M	M	M	M	L	L	L	L	L
Dipturus sp A	Longnose skate	*Rajidae*	N	Y	Y	Y	Shelf	Common	25	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Dipturus sp B	Grey Skate	*Rajidae*	Y	Y	Y	Y	Shelf	Sparse	13	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Dipturus sp J	Deepwater skate	*Rajidae*	Y	Y	Y	Y	Mid-slope	Sparse	16	H	L	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	M	L	L	L	L
Dipturus sp M	Pigmy thornback skate	*Rajidae*	Y	Y	Y	Y	Shelf	Rare	nd	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Dipturus sp P	Challenger Skate	*Rajidae*	Y	Y	Y	Y	Lower slope	Rare	nd	L	L	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Irolita waitii	Southern round skate	*Rajidae*	Y	N	N	N	Shelf	Rare	nd	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Notoraja sp A	Blue skate	*Rajidae*	Y	Y	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	M	L	L	L	L
Pavoraja nitida	Peacock skate	*Rajidae*	Y	Y	Y	Y	Shelf	Common	69	L	H	L	L	L	H	L	M	M	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Myliobatiformes	Eagle & devil rays and stingrays																																	
Dasyatis brevicaudata	Smooth Stingray	*Dasyatididae*	Y	Y	Y	Y	Shelf	Common	89	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Dasyatis thetidis	Black Stingray	*Dasyatididae*	Y	Y	Y	Y	Shelf	Common	96	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Myliobatis australis	Southern eagle ray	*Myliobatidae*	Y	Y	Y	Y	Self	Abundant	88	L	H	L	L	L	M	M	L	L	L	H	L	H	H	L	M	M	M	M	M	L	L	L	L	L
Trygonoptera mucosa	Western shovelnose stingaree	*Urolophidae*	Y	N	N	N	Shelf	Common	2	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Trygonoptera testacea	Common stingaree	*Urolophidae*	N	N	N	Y	Shelf	Common	31	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Trygonoptera sp B	Eastern shovelnose stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	Common	<1	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus bucculentus	Sandyback stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	Common	124	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus cruciatus	Banded stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	Common	70	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus expansus	Wide stingaree	*Urolophidae*	Y	N	N	N	Upper slope	Abundant	351	M	L	L	H	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	M	L	L	L	L
Urolophus gigas	Spotted stingaree	*Urolophidae*	Y	Y	Y	N	Shelf	Sparse	3	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus kapalensis	Kapala stingaree	*Urolophidae*	N	N	N	Y	Shelf	Sparse	1	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus orarius	Coastal stingaree	*Urolophidae*	Y	N	N	N	Shelf	Sparse	nd	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus paucimaculatus	Sparsely-spotted stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	Abundant	90	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus sufflavus	Yellowback stingaree	*Urolophidae*	N	N	N	Y	Shelf	Sparse	5	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Urolophus viridis	Green-backed stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	Abundant	455	L	H	L	L	L	H	L	L	L	L	H	L	H	H	L	M	L	L	L	L	L	L	L	L	L
Rhinobatiformes	Shovelnose and guitar rays																																	
Aptychotrema rostrata	Eastern shovelnose ray	*Rhinobatidae*	N	N	N	Y	Shelf	Common	23	M	L	L	L	L	H	L	M	M	L	H	L	H	M	L	M	L	L	L	L	M	L	L	L	L
Aptychotrema vincentiana	Western shovelnose ray	*Rhinobatidae*	Y	Y	N	N	Shelf	Sparse	7	L	M	L	L	L	H	L	M	M	L	H	L	H	M	L	M	L	L	L	L	L	L	L	L	L
Trygonorrhina fasciata	Southern fiddler ray	*Rhinobatidae*	Y	Y	Y	N	Shelf	Abundant	219	L	L	L	L	L	H	L	M	M	L	H	L	H	M	L	M	L	L	L	L	L	L	L	L	L
Trygonorrhina sp A	Eastern fiddler ray	*Rhinobatidae*	N	N	N	Y	Shelf	Rare	<1	M	L	L	L	L	H	L	M	M	L	H	L	H	M	L	M	L	L	L	L	M	L	L	L	L
Torpediniformes	Electric rays																																	
Hypnos monopterygium	Coffin ray	*Hypnidae*	Y	N	N	Y	Shelf	Sparse	9	M	M	L	L	L	H	L	M	L	L	H	L	H	H	M	M	L	L	L	L	M	L	L	L	L
Narcine tasmaniensis	Tasmanian numbfish	*Narcinidae*	Y	Y	Y	Y	Upper slope	Common	56	H	L	L	H	L	H	L	M	L	L	H	L	H	H	M	M	L	L	L	L	M	L	L	L	L
Torpedo macneilli	Short-tail torpedo ray	*Narcinidae*	Y	Y	Y	Y	Upper slope	Common	72	H	L	L	H	L	H	L	M	L	L	H	L	H	H	M	M	L	L	L	L	M	L	L	L	L
Holocephaliformes	Chimaeras																																	
Callorhinchus milii	Elephant fish	*Callorhinchidae*	Y	Y	Y	Y	Shelf	Abundant	48	L	H	L	L	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	L	H	L	L	L
Chimaera lignaria	Giant chimaera	*Callorhinchidae*	N	N	Y	N	Mid-slope	Rare	<1	H	L	L	L	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	L	L
Chimaera sp A	Southern chimaera	*Chimaeridae*	Y	Y	Y	Y	Upper slope	Sparse	12	H	L	L	H	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	M	L
Hydrolagus lemures	Blackfin Ghostshark	*Chimaeridae*	Y	Y	N	Y	Upper slope	Sparse	11	H	L	L	H	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	M	L
Hydrolagus ogilbyi	Ogilbys Ghostshark	*Chimaeridae*	Y	Y	Y	Y	Upper slope	Sparse	10	H	L	L	H	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	M	L
Hydrolagus sp A	Black ghostshark	*Chimaeridae*	N	Y	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	L	L
Hydrolagus sp C	Giant ghostshark	*Chimaeridae*	N	N	N	Y	Mid-slope	Rare	<1	H	L	L	L	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	L	L
Harriotta raleighana	Bigspine spookfish	*Rhinochimaeridae*	Y	Y	Y	Y	Mid-slope	Rare	<1	H	L	L	L	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	L	L
Rhinochimaera pacifica	Pacific spookfish	*Rhinochimaeridae*	Y	Y	Y	Y	Mid-slope	Rare	1	H	L	L	L	L	H	H	L	L	L	H	H	H	H	H	H	H	H	H	H	H	L	L	L	L

Table 6. Diet composition and trophic level of each species

The table excludes those species which have most of their distributional ranges outside south-eastern Australia. %M, percent mass of prey items, %V, percent volume of prey items; %O, percent frequency of occurrence; n, number of studies examining stomach contents; N, number of animals with prey items present in stomach contents; total, total number of animals inspected for stomach contents; Unsp, unspecified. "External" refers to an external study with published results relevant to the present study, including New South Wales Department of Primary Industries (NSW DPI) and the Western Australian Marine Research Laboratories (WAMRL). The present study includes the Marine and Freshwater Fisheries Research Institute (MAFFRI), CSIRO Marine and Atmospheric Research (CSIRO) and the universities of Adelaide, Deakin, Macquarie, Melbourne, Murdoch, and Tasmania.

Table 6 (continued)

Scientific name	Common name	Family	Sample size			Metric	Diet composition expressed as %M, %V or %O												Trophic level	Reference	Project laboratory and/or university
			n	N	Total		Mammal	Bird	Chond-richthyan	Teleost	Cephal-opod	Crust-acean	Invert-ebrate	Reptile	Zoo-plankton	Mollusc	Plant	Total			
Pelagic and semipelagic species																					
Lamniformes	Mackerel & thresher sharks																				
Alopias vulpinus	Thresher shark	*Alopiidae*	3	388		Unsp			1.0	26.7	71.8	0.5						100.0	4.20	Cortés (1999)	External
Isurus oxyrinchus	Shortfin mako	*Lamnidae*	7	453		Unsp	0.4		13.6	77.1	7.2	1.3		0.2			0.2	100.0	4.30	Cortés (1999)	External
Lamna nasus	Porbeagle	*Lamnidae*	4	115		Unsp		0.7		74.7	22.7		1.3				0.6	100.0	4.20	Cortés (1999)	External
Carcharhiniformes	Whaler & hammerhead sharks																				
Prionace glauca	Blue shark	*Carcharhinidae*	14	1293		Unsp	0.2	0.3	0.4	38.5	49.4	5.0	1.0		4.9	0.2		99.9	4.10	Cortés (1999)	External
Myliobatiformes																					
Manta birostris	Manta ray	*Mobulidae*	nd																		
Demersal species																					
Hexanchiformes	Sixgill & sevengill sharks																				
Chlamydoselachus anguineus	Frill shark	*Chlamydoselachidae*	1	38		Unsp				14.8	85.2							100.0	4.20	Cortés (1999)	External
Heptranchias perlo	Sharpnose sevengill shark	*Hexanchidae*	1	94		%M			0.5	91.8	7.3	0.3						99.9	4.23	Braccini (in preparation)	MAFFRI
Hexanchus nakamurai	Bigeye sixgill shark	*Hexanchidae*	nd																		
Hexanchus griseus	Bluntnose sixgill shark	*Hexanchidae*	4	106		Unsp	8.9		10.7	22.9	57.0					0.3		99.8	4.30	Cortés (1999)	External
Notorynchus cepedianus	Broadnose sevengill shark	*Hexanchidae*	1	114		%M	5.9		64.2	24.9	4.9	0.1						100.0	4.55	Braccini (in preparation)	MAFFRI
Squaliformes	Dogfishes																				
Echinorhinus brucus	Bramble shark	*Echinorhinidae*	nd																		
Oxynotus bruniensis	Prickly dogfish	*Echinorhinidae*	nd																		
Centrophorus harrissoni	Harrissons dogfish	*Squalidae*	1	78	116	%O				83.0	16.0	1.0						100.0	4.23	Daley et al. (2002)	External (DPI NSW)
Centrophorus moluccensis	Endeavour dogfish	*Squalidae*	1	10	11	%O				50.0	33.3	16.7						100.0	4.11	Daley et al. (2002)	External (DPI NSW)
Centrophorus zeehani	Southern dogfish	*Squalidae*	1	8		%M				95.0	5.0							100.0	4.24	Unpublished data	MAFFRI
Centroscyllium kamoharai	Bareskin dogfish	*Squalidae*	1	12	100	%O				27.2	45.7	27.2						100.0	4.03	Daley et al. (2002)	External (DPI NSW)
Centroscymnus crepidater	Golden dogfish	*Squalidae*	1	67	148	%O				56.3	35.4	8.3						100.0	4.17	Daley et al. (2002)	External (DPI NSW)
Centroscymnus coelolepsis	Portugese dogfish	*Squalidae*	1	34	94	%O	21.9			45.3	32.8							100.0	4.40	Daley et al. (2002)	External (DPI NSW)
Centroscymnus owstoni	Owstons dogfish	*Squalidae*	1	115	230	%O				21.7	78.3							100.0	4.21	Daley et al. (2002)	External (DPI NSW)
Centroscymnus plunketi	Plunkets dogfish	*Squalidae*	1	35	46	%O			19.3	64.8	15.9							100.0	4.31	Daley et al. (2002)	External (DPI NSW)
Cirrhigaleus barbifer	Mandarin shark	*Squalidae*	nd																		
Dalatias licha	Black shark	*Squalidae*	1	14		%M			7.2	92.8								100.0	4.27	Unpublished data	MAFFRI
Deania calcea	Brier shark	*Squalidae*	1	143	409	%O				85.1	14.9							100.0	4.23	Daley et al. (2002)	External (DPI NSW)
Deania quadrispinosa	Longsnout dogfish	*Squalidae*	1	80	108	%O				98.9	1.1							100.0	4.24	Daley et al. (2002)	External (DPI NSW)
Etmopterus baxteri	Giant latern shark	*Squalidae*	1	117		Unsp				70.6	26.9	2.3	0.2					100.0	4.20	Cortés (1999)	External
Etmopterus bigelowi	Smooth lantern shark	*Squalidae*	nd																		
Etmopterus granulosus	Southern lantern shark	*Squalidae*	1	103	369	%O				98.9	1.1							100.0	4.24	Daley et al. (2002)	External (DPI NSW)
Etmopterus lucifer	Blackbelly lantern shark	*Squalidae*	1	24		%M				73.2	12.2		14.6					100.0	4.13	Daley (unpublished data)	CSIRO
Etmopterus pusillus	Slender Lantern shark	*Squalidae*	1	5		Unsp				40.0	60.0							100.0	4.20	Cortés (1999)	External
Etmopterus sp B	Bristled latern shark	*Squalidae*	1	71	221	%O				12.6	86.3	1.1						100.0	4.20	Daley et al. (2002)	DPINSW
Isistius brasiliensis	Cookie-cutter shark	*Squalidae*	nd																		
Somniosus pacificus	Pacific sleeper shark	*Squalidae*	6	13		Unsp	16.7			33.3	38.9	5.6				5.6		100.1	4.20	Cortés (1999)	External
Squalus acanthias	White-spotted spurdog	*Squalidae*	1	4		%M				25.1		74.9						100.0	3.70	Unpublished data	MAFFRI
Squalus chloroculus	Green-eyed spurdog	*Squalidae*	1	33		%M			11.8	72.4	15.8							100.0	4.28	Unpublished data	MAFFRI
Squalus megalops	Piked spurdog	*Squalidae*	1	574		%M			5	38.3	52.4	2.1	0.8					98.2	4.16		MAFFRI, Adelaide

Table 6 (continued)

Scientific name	Common name	Family	Sample size			Metric	Diet composition expressed as %M, %V or %O												Trophic level	Reference	Project laboratory and/or university
			n	N	Total		Mammal	Bird	Chond-richthyan	Teleost	Cephal-opod	Crust-acean	Invert-ebrate	Reptile	Zoo-plankton	Mollusc	Plant	Total			
Pristiophoriformes	Sawsharks																				
Pristiophorus cirratus	Common sawshark	*Pristiophoridae*	nd																		
Pristiophorus nudipinnis	Southern sawshark	*Pristiophoridae*	nd																		
Pristiophorus sp A	Eastern sawshark	*Pristiophoridae*	nd																		
Squatiniformes	Angel sharks																				
Squatina australis	Australian angel shark	*Squatinidae*	1	51		%M				85.7	11.4	2.9						100.0	4.21	Unpublished data	MAFFRI
Squatina tergocellata	Ornate angel shark	*Squatinidae*	1	127		%O				59.0	69.0								4.20	Bridge *et al.* (1998)	External
Squatina sp A	Eastern angel shark	*Squatinidae*	1	21		%M			0.9	98.9		0.2						100.0	4.24	Unpublished data	MAFFRI
Heterodontiformes	Horn sharks																				
Heterodontus galeatus	Crested horn shark	*Heterodontidae*	nd																		
Heterodontus portusjacksoni	Port Jackson shark	*Heterodontidae*	1	29		%M				20.8	0.8	27.0	0.8			50.3	0.30	100.0	3.46	Unpublished data	MAFFRI
Orectolobiformes	Catsharks, wobbegongs, carpet																				
Brachaelurus waddi	Blind Shark	*Brachaeluridae*	nd																		
Orectolobus halei	Ornate wobbegong	*Orectolobidae*	1	41	201	%M			12.5	79.5	8.0							100.0	4.29	Huveneers (2007)	Macquarie
Orectolobus maculatus	Spotted wobbegong	*Orectolobidae*	1	39	155	%M			6.7	78.8	14.5							100.0	4.26	Huveneers (2007)	Macquarie
Orectolobus ornatus	Dwarf wobbegong	*Orectolobidae*	1	64	285	%M				86.5	13.5							100.0	4.23	Huveneers (2007)	Macquarie
Sutorectus tentaculatus	Cobbler wobbegong	*Orectolobidae*	nd																		
Parascyllium collare	Collared carpet shark	*Parascylliidae*	nd																		
Parascyllium ferrugineum	Rusty carpet shark	*Parascylliidae*	1	20		%M				0.8	1.0		98.2					100.0	3.51	D. Mossop (unpublished data)	MAFFRI, Melbourne
Parascyllium variolatum	Varied carpet shark	*Parascylliidae*	nd																		
Apristurus sp A	Freckled catshark	*Scyliorhinidae*	nd																		
Apristurus sp C	Fleshynose catshark	*Scyliorhinidae*	nd																		
Apristurus sp D	Roughskin catshark	*Scyliorhinidae*	1	21		%M				84.5	0.1	6.6	8.8					100.0	4.13	R. Daley (unpublished data)	CSIRO
Apristurus sp E	Bulldog catshark	*Scyliorhinidae*	nd																		
Apristurus sp G	Pinocchio catshark	*Scyliorhinidae*	nd																		
Asymbolus analis	Grey spotted catshark	*Scyliorhinidae*	nd																		
Asymbolus occiduus	Western spotted catshark	*Scyliorhinidae*	nd																		
Asymbolus rubiginosus	Orange spotted catshark	*Scyliorhinidae*	1	10		%M				24.9	21.8	53.3						100.0	3.85	D. Mossop (unpublished data)	MAFFRI, Melbourne
Asymbolus vincenti	Gulf catshark	*Scyliorhinidae*	nd																		
Cephaloscyllium laticeps	Draughtboard shark	*Scyliorhinidae*	1	400		%M				11.0	7.0	63.0				19.0		100.0	3.95	C. Awruch (unpublished data)	Tasmania
Cephaloscyllium sp A	Whitefinned swell shark	*Scyliorhinidae*	1	26		%M			19.9	76.5		2.3	1.3					100.0	4.30	Unpublished data	MAFFRI
Galeus boardmani	Sawtail shark	*Scyliorhinidae*	1	74		%M				89.4	4.5	5.9	0.2					100.0	4.19	Daley (unpublished data)	CSIRO
Lamniformes	Mackerel & thresher sharks																				
Carcharidon carcharias	White shark	*Lamnidae*	14	259		Unsp	21.1	1.1	35.7	35.3	3.6	1.8	0.4	0.4		0.4		99.8	4.53	Cortés (1999)	External
Carcharias taurus	Grey nurse shark	*Odontaspididae*	5	70		Unsp			31.2	65.9	2.9	0.1						100.1	4.37	Cortés (1999)	External
Odontaspis ferox	Smalltooth sandtiger shark	*Odontaspididae*	nd																		
Mitsukurina owstoni	Goblin shark	*Mitsukurinidae*	1	148		%M				43.4	3.8	4.3							4.20	Yano *et al.* (2007)	External
Carcharhiniformes	Whaler & hammerhead sharks																				
Carcharhinus brachyurus	Bronze Whaler	*Carcharhinidae*	4	608		Unsp	0.2		1.9	78.9	19.0							100.0	4.20	Cortés (1999)	External
Carcharhinus obscurus	Dusky Shark	*Carcharhinidae*	1	1322	3176	%O			1.5	51.8	46.4	0.3						100.0	4.23	Simpfendorfer et al. (2001)	External (WAMRL)
Sphyrna zygaena	Smooth hammerhead	*Sphyrnidae*	1	42		%O				41.1	57.1	1.8						100.0	4.20	Stevens (1984)	External (CSIRO)
Furgaleus macki	Whiskery Shark	*Triakidae*	1	372	1491	%O				4.7	94.5	0.8						100.0	4.20	Simpfendorfer et al. (2001)	External (WAMRL)
Galeorhinus galeus	School Shark	*Triakidae*	1	169	218	%M			0.6	56.1	43.2	0.1	0.1			0.1		100.0	4.22	Walker (1986)	External (MAFFRI)
Hypogaleus hyugaensis	Pencil Shark	*Triakidae*	1	46		%O				82.0	18.0							100.0	4.23	Simpfendorfer et al. (2002)	External (WAMRL)
Mustelus antarcticus	Gummy Shark	*Triakidae*	1	435	497	%M			0.3	15.5	48.8	33.6	0.8			1.1		100.0	3.96	Walker (1986)	External (MAFFRI)
Mustelus sp B	White-spotted Gummy Shark	*Triakidae*	nd																		

Table 6 (continued)

Scientific name	Common name	Family	Sample size			Metric	Diet composition expressed as %M, %V or %O												Trophic level	Reference	Project laboratory and/or university
			n	N	Total		Mammal	Bird	Chond-richthyan	Teleost	Cephal-opod	Crust-acean	Invert-ebrate	Reptile	Zoo-plankton	Mollusc	Plant	Total			
Rajiformes	Skates																				
Amblyraja hyperborea	Boreal skate	*Rajidae*	nd																		
Dipturus australis	Sydney skate	*Rajidae*	nd																		
Dipturus cerva	White-spotted skate	*Rajidae*	1	160	166	%M			2.3	9.1	1.8	86.5				0.2		99.9	3.62	Treloar et al. (2007)	CSIRO, Deakin
Dipturus gudgeri	Bight skate	*Rajidae*	1	72	263	%M				78.0	0.2	21.8						100.0	4.08	Treloar et al. (2007)	CSIRO, Deakin
Dipturus lemprieri	Thornback skate	*Rajidae*	1	72	77	%M			0.6	18.4	5.0	75.7						99.7	3.69	Treloar et al. (2007)	CSIRO, Deakin
Dipturus whitleyi	Melbourne skate	*Rajidae*	1	48	60	%M			1.1	42.4	27.0	29.5						100.0	4.02	Treloar et al. (2007)	CSIRO, Deakin
Dipturus sp A	Longnose skate	*Rajidae*	1	335	410	%M			0.2	46.3	26.1	27.2						99.8	4.03	Treloar et al. (2007)	CSIRO, Deakin
Dipturus sp B	Grey skate	*Rajidae*	1	37	113	%M			0.1	1.0		98.9						100.0	3.53	Treloar et al. (2007)	CSIRO, Deakin
Dipturus sp J	Deepwater skate	*Rajidae*	1	5		%M				61.0		39.0						100.0	3.96	Unpublished data	MAFFRI
Dipturus sp M	Pigmy thornback skate	*Rajidae*	nd																		
Dipturus sp P	Challenger Skate	*Rajidae*	nd																		
Irolita waitii	Southern round skate	*Rajidae*	nd																		
Notoraja sp A	Blue skate	*Rajidae*	nd																		
Pavoraja nitida	Peacock skate	*Rajidae*	1	33	33	%M				1.6		97.7	0.7					100.0	3.53	M. A. Treloar (Unpublished data)	CSIRO, Deakin
Myliobatiformes	Eagle & devil rays and stingrays																				
Dasyatis brevicaudata	Smooth Stingray	*Dasyatididae*	1	2		%M					98.1	1.9						100.0	4.19	D. Phillips (unpublished data)	MAFFRI, Deakin
Dasyatis thetidis	Black Stingray	*Dasyatididae*	nd																		
Myliobatis australis	Southern eagle ray	*Myliobatidae*	1	93		%M				0.2		25.6	10.8			63.3		99.9	3.25	Unpublished data	MAFFRI
Trygonoptera mucosa	Western shovelnose stingaree	*Urolophidae*	1			%O				0.7		52.5	95.7			2.8			3.50	Platell *et al.* (1998)	External
Trygonoptera testacea	Common stingaree	*Urolophidae*	nd																		
Trygonoptera sp B	Eastern shovelnose stingaree	*Urolophidae*	1	22		%V							100.0					100.0	3.50	Unpublished data	MAFFRI
Urolophus bucculentus	Sandyback stingaree	*Urolophidae*	1	38		%V				4.7	5.5	89.1				0.6		99.9	3.59	Unpublished data	MAFFRI
Urolophus cruciatus	Banded stingaree	*Urolophidae*	1	51		%V						25.2	72.9			1.9		100.0	3.50	Unpublished data	MAFFRI
Urolophus expansus	Wide stingaree	*Urolophidae*	1	7		%V						82.7	17.3					100.0	3.52	Unpublished data	MAFFRI
Urolophus gigas	Spotted stingaree	*Urolophidae*	1	8		%V				23.0		77.0						100.0	3.69	Unpublished data	MAFFRI
Urolophus kapalensis	Kapala stingaree	*Urolophidae*	nd																		
Urolophus ovarius	Coastal stingaree	*Urolophidae*	nd																		
Urolophus paucimaculatus	Sparsely-spotted stingaree	*Urolophidae*	1	101		%V				4.1		91.1	4.8			0.1		100.1	3.55	Unpublished data	MAFFRI
Urolophus sufflavus	Yellowback stingaree	*Urolophidae*	nd																		
Urolophus viridis	Green-backed stingaree	*Urolophidae*	1	45		%V				1.1		89.6	8.6			1.1		100.4	3.53	Unpublished data	MAFFRI
Rhinobatiformes	Shovelnose and guitar rays																				
Aptychotrema rostrata	Eastern shovelnose ray	*Rhinobatidae*	1	76		%V				20.1	0.44	79.46						100	3.59	Kyne and Bennett (2002b)	External
Aptychotrema vincentiana	Western shovelnose ray	*Rhinobatidae*	nd																		
Trygonorrhina fasciata	Southern fiddler ray	*Rhinobatidae*	1	261	275	%V			0.6	17.2	2.8	73.4	5.3				0.8	100.1	3.66	Marshall, L. et al. (2007)	Murdoch
Trygonorrhina sp A	Eastern fiddler ray	*Rhinobatidae*	nd																		
Torpediniformes	Electric rays																				
Hypnos monopterygium	Coffin ray	*Hypnidae*	nd																		
Narcine tasmaniensis	Tasmanian numbfish	*Narcinidae*	1	33		%M						15.6	84.4					100	3.50	Daley (unpublished data)	CSIRO
Torpedo macneilli	Short-tail torpedo ray	*Narcinidae*	1	2		%M				98.8		1.2						100	4.23	Unpublished data	MAFFRI
Holocephaliformes	Chimaeras																				
Callorhinchus milii	Elephant fish	*Callorhinchidae*	1	59		%M				60.8		3.0	4.9			31.3		100.0	3.83	Unpublished data	MAFFRI
Chimaera lignaria	Giant chimaera	*Callorhinchidae*	1	66		%M				25.7		19.1	47.3			7.9		100.0	3.66	Daley (unpublished data)	CSIRO
Chimaera sp A	Southern chimaera	*Chimaeridae*	1	35		%M				5.1	25.1	56.4	1.5			11.9		100.0	3.68	Unpublished data	MAFFRI
Hydrolagus lemures	Blackfin Ghostshark	*Chimaeridae*	1	14		%M				32.6	22.8	35.6	9.0					100.0	3.91	Unpublished data	MAFFRI
Hydrolagus ogilbyi	Ogilbys Ghostshark	*Chimaeridae*	1	22		%M				68.9		22.1	6.6			2.3		99.9	4.00	Unpublished data	MAFFRI
Hydrolagus sp A	Black ghostshark	*Chimaeridae*	1	9		%M				25.2		48.1	9.8			17.0		100.1	3.63	Unpublished data	MAFFRI
Hydrolagus sp C	Giant ghostshark	*Chimaeridae*	1	2		%M			42.4			57.6						100.0	4.00	Unpublished data	MAFFRI
Harriotta raleighana	Bigspine spookfish	*Rhinochimaeridae*	nd																		
Rhinochimaera pacifica	Pacific spookfish	*Rhinochimaeridae*	1	14		%M				60.0		40.0						100.0	3.95	Unpublished data	MAFFRI

[A] Common before fishing; [B] Abundant before fishing; [C] Historically H (high) when targeted.

Table 7. Ecological risk assessment for each species

Distribution: SA, South Australia, BS, Bass Strait; Tas, Tasmania; NSW, New South Wales; Y, yes; N, no; ISMP, Integrated Scientific Monitoring Program. Risk: L, low; M, medium; H, high; V, very high.

Table 7 (continued)

Scientific name	Common name	Family	Distribution				Depth stratum	Abundance based on catch				Abundance trend				Catch susceptibility risk					Biological productivity				Trophic position	
			SA	BS	Tas	NSW		ISMP Depth (m)	ISMP catch (t)	Category	Risk	ISMP trend long term	ISMP trend 2000–06	ISMP 2000–06 decline	Risk	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Max age (y)	Risk	Reprod- uction	Risk	Value	Risk
Pelagic and semipelagic species																										
Lamniformes	Mackerel & thresher sharks																									
Alopias vulpinus	Thresher shark	*Alopiidae*	Y	Y	Y	Y	Shelf, oceanic	200–599	16	Common	L					L	L	L	L	L	22	H		H	4.20	M
Isurus oxyrinchus	Shortfin mako	*Lamnidae*	Y	Y	Y	Y	Shelf, oceanic	200–599	2	Common	L					L	L	L	L	L	29	H		H	4.30	H
Lamna nasus	Porbeagle	*Lamnidae*	Y	Y	Y	Y	Shelf, oceanic	200–599	<1	Rare	H					L	L	L	L	L	25	H		H	4.20	M
Carcharhiniformes	Whaler & hammerhead sharks																									
Prionace glauca	Blue shark	*Carcharhinidae*	Y	Y	Y	Y	Shelf, oceanic	200–599	<1	Abundant	L					L	L	L	L	L	12	M			4.10	M
Myliobatiformes																										
Manta birostris	Manta ray	*Mobulidae*	N	N	N	Y	Shelf, oceanic	nd	nd	Common	L					L	L	L	L	L						
Demersal species																										
Hexanchiformes	Sixgill & sevengill sharks																									
Chlamydoselachus anguineus	Frill shark	*Chlamydoselachidae*	N	Y	Y	Y	Mid-slope	≥600	<1	Rare	H					M	L	L	L	L					4.20	M
Heptranchias perlo	Sharpnose sevengill shark	*Hexanchidae*	Y	Y	Y	Y	Upper slope	200–599	19	Sparse	M					M	L	L	H	L					4.23	M
Hexanchus nakamurai	Bigeye sixgill shark	*Hexanchidae*	N	N	N	Y	Mid-slope	nd	nd	Rare	H					M	L	L	M	L						
Hexanchus griseus	Bluntnose sixgill shark	*Hexanchidae*	N	Y	Y	Y	Entire slope	<200	<1	Rare	H					M	L	L	L	L					4.30	H
Notorynchus cepedianus	Broadnose sevengill shark	*Hexanchidae*	Y	Y	Y	Y	Shelf	<200	3	Common	M					L	M	L	L	L	32	H			4.55	H
Squaliformes	Dogfishes																									
Echinorhinus brucus	Bramble shark	*Echinorhinidae*	Y	Y	N	N	Mid-slope	nd	nd	Rare	H					M	L	L	L	L						
Oxynotus bruniensis	Prickly dogfish	*Echinorhinidae*	Y	Y	N	N	Upper slope	200–599	1	Sparse	M					H	L	L	L	L						
Centrophorus harrissoni	Harrissons dogfish	*Squalidae*	N	Y	N	Y	Upper slope	200–599	<1	Rare	H	No trend	No trend	0.273	H	H	L	L	H	L	39	H		H	4.23	M
Centrophorus moluccensis	Endeavour dogfish	*Squalidae*	N	Y	N	Y	Upper slope	200–599	30	Common	L	No trend	No trend	0.273	H	H	L	L	H	L					4.11	M
Centrophorus zeehani	Southern dogfish	*Squalidae*	Y	Y	Y	Y	Upper slope	200–599	12	Sparse	M	No trend	No trend	0.273	H	H	L	L	H	L	37	H		H	4.24	M
Centroscyllium kamoharai	Bareskin dogfish	*Squalidae*	N	N	N	Y	Mid-slope	nd	nd	Rare	H					H	L	L	H	L					4.03	M
Centroscymnus crepidater	Golden dogfish	*Squalidae*	Y	Y	Y	Y	Mid-slope	≥600	56	Common	L	Indeterminable	Indeterminable			M	L	L	L	L	54	H		H	4.17	M
Centroscymnus coelolepsis	Portugese dogfish	*Squalidae*	Y	Y	Y	Y	Mid-slope	200–599	1	Sparse	M					M	L	L	L	L					4.40	H
Centroscymnus owstoni	Owstons dogfish	*Squalidae*	Y	Y	Y	Y	Mid-slope	≥600	71	Common	L	Decreasing	No trend	1.578	L	M	L	L	L	L	29	H		H	4.21	M
Centroscymnus plunketi	Plunkets dogfish	*Squalidae*	N	Y	Y	Y	Mid-slope	≥600	<1	Rare	H					M	L	L	L	L	30	H		H	4.31	H
Cirrhigaleus barbifer	Mandarin shark	*Squalidae*	N	N	N	Y	Mid-slope	nd	nd	Rare	H					M	L	L	L	L						
Dalatias licha	Black shark	*Squalidae*	Y	Y	Y	Y	Mid-slope	≥600	81	Common	L	Decreasing	Decreasing	0.204	H	M	L	L	L	L					4.27	H
Deania calcea	Brier shark	*Squalidae*	Y	Y	Y	Y	Mid-slope	≥600	257	Abundant	L	Decreasing	Decreasing	0.476	M	M	L	L	L	L	36	H		H	4.23	M
Deania quadrispinosa	Longsnout dogfish	*Squalidae*	Y	Y	Y	Y	Upper slope	≥600	4	Sparse	M					H	L	L	L	L					4.24	M
Etmopterus baxteri	Giant latern shark	*Squalidae*	N	Y	Y	Y	Mid-slope	nd	nd	Rare	H					M	L	L	L	L	58	H		H	4.20	M
Etmopterus bigelowi	Smooth lantern shark	*Squalidae*	N	N	Y	Y	Mid-slope	≥600	<1	Rare	H					M	L	L	L	L						
Etmopterus granulosus	Southern lantern shark	*Squalidae*	N	Y	Y	Y	Mid-slope	≥600	15	Sparse	M					M	L	L	L	L	19	H			4.24	M
Etmopterus lucifer	Blackbelly lantern shark	*Squalidae*	N	N	N	Y	Mid-slope	≥600	5	Sparse	M					M	L	L	L	L					4.13	M
Etmopterus pusillus	Slender Lantern shark	*Squalidae*	N	Y	Y	Y	Mid-slope	≥600	4	Sparse	M					M	L	L	L	L	17	H			4.20	M
Etmopterus sp B	Bristled latern shark	*Squalidae*	Y	Y	Y	Y	Lower slope	nd	nd	Rare	H					M	L	L	L	L					4.20	M
Isistius brasiliensis	Cookie-cutter shark	*Squalidae*	N	Y	Y	Y	Lower slope	nd	nd	Rare	H					M	L	L	L	L						
Somniosus pacificus	Pacific sleeper shark	*Squalidae*	N	N	Y	N	Mid-slope	nd	nd	Rare	H					M	L	L	L	L					4.20	M
Squalus acanthias	White-spotted spurdog	*Squalidae*	N	Y	Y	N	Shelf	200–599	4	Sparse	M					L	L	L	L	L	80	H			3.70	L
Squalus chloroculus	Green-eyed spurdog	*Squalidae*	Y	Y	Y	Y	Upper slope	200–599	212	Abundant	L	Decreasing	Decreasing	0.123	H	H	L	L	H	L	36	H		H	4.28	H
Squalus megalops	Spikey spurdog	*Squalidae*	Y	Y	Y	Y	Shelf	200–599	719	Abundant	L	Increasing	Increasing	2.643	L	L	L	L	L	L	28	H		H	4.16	M
Zameus squamulosus	Velvet dogfish	*Squalidae*	N	Y	Y	Y	Lower slope	≥600	<1	Rare	H					M	L	L	L	L						

Table 7 (continued)

Scientific name	Common name	Family	Distribution				Depth stratum	Abundance based on catch				Abundance trend				Catch susceptibility risk					Biological productivity				Trophic position	
			SA	BS	Tas	NSW		ISMP Depth (m)	ISMP catch (t)	Category	Risk	ISMP trend long term	ISMP trend 2000–06	ISMP 2000–06 decline	Risk	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Max age (y)	Risk	Reprod-uction	Risk	Value	Risk
Pristiophoriformes	Sawsharks																									
Pristiophorus cirratus	Common sawshark	*Pristiophoridae*	Y	Y	Y	N	Shelf	<200	276	Abundant	L	Decreasing	Decreasing	0.556	M	L	H	L	L	L	15	M		M		
Pristiophorus nudipinnis	Southern sawshark	*Pristiophoridae*	Y	Y	Y	N	Shelf	<200	32	Common	L	Indeterminable	Indeterminable			L	M	L	L	L	9	M		M		
Pristiophorus sp A	Eastern sawshark	*Pristiophoridae*	N	N	N	Y	Shelf	nd	nd	Sparse	M					M	L	L	L	L						
Squatiniformes	Angel sharks																									
Squatina australis	Australian angel shark	*Squatinidae*	Y	Y	Y	Y	Shelf	<200	311	Abundant	L	Decreasing	No trend	0.657	M	L	L	L	L	L					4.21	M
Squatina tergocellata	Ornate angel shark	*Squatinidae*	Y	N	N	N	Shelf	<200	289	Abundant	L		No trend	1.643	L	M	L	L	L	L					4.20	M
Squatina sp A	Eastern angel shark	*Squatinidae*	N	R	N	Y	Shelf	200–599	<1	Sparse	M					H	L	L	L	L					4.24	M
Heterodontiformes	Horn sharks																									
Heterodontus galeatus	Crested horn shark	*Heterodontidae*	N	N	N	Y	Shelf	<200	<1	Rare	H					L	L	L	L	L						
Heterodontus portusjacksoni	Port Jackson shark	*Heterodontidae*	Y	Y	Y	Y	Shelf	<200	211	Abundant	L	No trend	Decreasing	0.687	L	L	L	L	L	L	35	H		H	3.46	L
Orectolobiformes	Catsharks, wobbegongs, carpet																									
Brachaelurus waddi	Blind Shark	*Brachaeluridae*	N	N	N	Y	Shelf	200–599	<1	Rare	H					L	L	L	L	L	27	H		H		
Orectolobus halei	Ornate wobbegong	*Orectolobidae*	Y	Y	N	Y	Shelf	nd	nd	Abundant	L					L	L	L	L	L	22	H		H	4.29	H
Orectolobus maculatus	Spotted wobbegong	*Orectolobidae*	Y	Y	N	Y	Shelf	<200	24	Abundant	L	Indeterminable	Indeterminable			L	L	L	L	L	20	H		H	4.26	H
Orectolobus ornatus	Dwarf wobbegong	*Orectolobidae*	N	N	N	Y	Shelf	<200	<1	Common	L					M	L	M	L	L					4.23	M
Sutorectus tentaculatus	Cobbler wobbegong	*Orectolobidae*	Y	N	N	N	Shelf	nd	nd	Rare	H					L	L	L	L	L						
Parascyllium collare	Collared carpet shark	*Parascylliidae*	N	Y	N	Y	Shelf	<200	10	Common	L					L	L	L	L	L						
Parascyllium ferrugineum	Rusty carpet shark	*Parascylliidae*	Y	Y	Y	N	Shelf	<200	19	Common	L					L	L	L	L	L					3.51	L
Parascyllium variolatum	Varied carpet shark	*Parascylliidae*	Y	Y	Y	N	Shelf	nd	nd	Common	L					L	L	L	L	L						
Apristurus sp A	Freckled catshark	*Scyliorhinidae*	Y	Y	Y	Y	Mid-slope	nd	nd	Rare	H					M	L	L	L	L						
Apristurus sp C	Fleshynose catshark	*Scyliorhinidae*	Y	Y	Y	Y	Mid-slope	≥600	<1	Rare	H					M	L	L	L	L						
Apristurus sp D	Roughskin catshark	*Scyliorhinidae*	Y	N	Y	N	Mid-slope	nd	nd	Rare	H					M	L	L	L	L					4.13	M
Apristurus sp E	Bulldog catshark	*Scyliorhinidae*	N	Y	Y	Y	Lower slope	nd	nd	Rare	H					L	L	L	L	L						
Apristurus sp G	Pinocchio catshark	*Scyliorhinidae*	Y	Y	Y	Y	Mid-slope	≥600	<1	Rare	H					M	L	L	L	L						
Asymbolus analis	Grey spotted catshark	*Scyliorhinidae*	N	N	N	Y	Shelf	<200	26	Common	L	No trend	No trend	0.675	L	L	L	L	L	L						
Asymbolus occiduus	Western spotted catshark	*Scyliorhinidae*	Y	N	N	N	Shelf	<200	<1	Rare	H					L	L	L	L	L						
Asymbolus rubiginosus	Orange spotted catshark	*Scyliorhinidae*	N	Y	Y	Y	Shelf	200–599	<1	Rare	H					L	L	L	L	L					3.85	L
Asymbolus vincenti	Gulf catshark	*Scyliorhinidae*	Y	Y	Y	?	Shelf	<200	<1	Rare	H					L	L	L	L	L						
Cephaloscyllium laticeps	Draughtboard shark	*Scyliorhinidae*	Y	Y	Y	Y	Shelf	<200	227	Abundant	L	No trend	No trend	0.864	L	L	L	L	L	L					3.95	L
Cephaloscyllium sp A	Whitefinned swell shark	*Scyliorhinidae*	Y	Y	Y	Y	Upper slope	200–599	385	Abundant	L	Decreasing	Decreasing	0.508	M	M	L	L	L	L	27	H		H	4.30	H
Galeus boardmani	Sawtail shark	*Scyliorhinidae*	Y	Y	Y	Y	Upper slope	200–599	23	Common	L	Decreasing	No trend	0.903	L	M	L	L	L	L					4.19	M
Lamniformes	Mackerel & thresher sharks																									
Carcharidon carcharias	White shark	*Lamnidae*	Y	Y	Y	Y	Shelf	<200	2	Sparse	M					L	M	L	L	L	13	M			4.53	H
Mitsukurina owstoni	Goblin shark	*Mitsukurinidae*	Y	Y	N	Y	Mid-slope	nd	nd	Rare	H					L	L	L	L	L					4.20	M
Carcharias taurus	Grey nurse shark	*Odontaspididae*	Y	Y	N	Y	Shelf	<200	3	Rare	H					M	L	L	L	L	17	H			4.37	H
Odontaspis ferox	Smalltooth sandtiger shark	*Odontaspididae*	N	N	N	Y	Shelf	200–599	4	Sparse	M					M	L	L	L	L						
Carcharhiniformes	Whaler & hammerhead sharks																									
Carcharhinus brachyurus	Bronze Whaler	*Carcharhinidae*	Y	Y	N	Y	Shelf	<200	17	Common	L					L	M	L	L	L	25	H			4.20	M
Carcharhinus obscurus	Dusky Shark	*Carcharhinidae*	Y	Y	Y	Y	Shelf	nd	nd	Common	L					L	M	L	L	L	32	H			4.23	M
Sphyrna zygaena	Smooth hammerhead	*Sphyrnidae*	Y	Y	Y	Y	Shelf	<200	3	Common	L					L	M	L	L	L					4.20	M
Furgaleus macki	Whiskery Shark	*Triakidae*	Y	R	R	N	Shelf	<200	<1	Common^B	L					L	H	L	L	L	11	M			4.20	M
Galeorhinus galeus	School Shark	*Triakidae*	Y	Y	Y	Y	Shelf	200–599	35	Abundant	L	Decreasing	Decreasing	0.426	M	L	H	L	M	L	42	H		H	4.22	M
Hypogaleus hyugaensis	Pencil Shark	*Triakidae*	Y	R	R	R	Shelf	nd	nd	Sparse	M					L	M	L	L	L					4.23	M
Mustelus antarcticus	Gummy Shark	*Triakidae*	Y	Y	Y	Y	Shelf	<200	186	Abundant	L	No trend	Decreasing	0.520	M	L	H	L	L	L	16	M		M	3.96	L
Mustelus sp B	White-spotted Gummy Shark	*Triakidae*	N	N	N	Y	Shelf	<200	<1	Rare	H					L	L	L	L	L						

Table 7 (continued)

Scientific name	Common name	Family	Distribution				Depth stratum	Abundance based on catch				Abundance trend				Catch susceptibility risk					Biological productivity				Trophic position	
			SA	BS	Tas	NSW		ISMP Depth (m)	ISMP catch (t)	Category	Risk	ISMP trend long term	ISMP trend 2000–06	ISMP 2000–06 decline	Risk	Otter trawl	Shark gillnet	Shark hook	Auto hook	Trap/ pot	Max age (y)	Risk	Reprod- uction	Risk	Value	Risk
Rajiformes	Skates																									
Amblyraja hyperborea	Boreal skate	*Rajidae*	?	Y	Y	N	Shelf	200–599	<1	Rare	H					L	L	L	L	L						
Dipturus australis	Sydney skate	*Rajidae*	N	N	N	Y	Shelf	<200	157	Abundant	L	No trend		0.721	L	M	L	L	L	L						
Dipturus cerva	White-spotted skate	*Rajidae*	Y	Y	Y	Y	Shelf	<200	37	Common	L	Indeterminable				L	L	L	L	L	9	M		M	3.62	L
Dipturus gudgeri	Bight skate	*Rajidae*	Y	Y	Y	Y	Upper slope	200–599	88	Common	L	Increasing		2.232	L	M	L	L	L	L	18	H		H	4.08	M
Dipturus lemprieri	Thornback skate	*Rajidae*	N	Y	Y	Y	Shelf	<200	19	Sparse	M					L	L	L	L	L					3.69	L
Dipturus whitleyi	Melbourne skate	*Rajidae*	Y	Y	Y	Y	Shelf	<200	176	Abundant	L	Increasing		2.233	L	L	L	L	L	L	16	M		M	4.02	M
Dipturus sp A	Longnose skate	*Rajidae*	N	Y	Y	Y	Shelf	<200	25	Common	L	Indeterminable				L	L	L	L	L	12	M		M	4.03	M
Dipturus sp B	Grey skate	*Rajidae*	Y	Y	Y	Y	Shelf	200–599	13	Sparse	M					L	L	L	L	L					3.53	L
Dipturus sp J	Deepwater skate	*Rajidae*	Y	Y	Y	Y	Mid-slope	200–599	16	Sparse	M					M	L	L	L	L					3.96	L
Dipturus sp M	Pigmy thornback skate	*Rajidae*	Y	Y	Y	Y	Shelf	nd	nd	Rare	H					L	L	L	L	L						
Dipturus sp P	Challenger Skate	*Rajidae*	Y	Y	Y	Y	Lower slope	nd	nd	Rare	H					L	L	L	L	L						
Irolita waitii	Southern round skate	*Rajidae*	Y	N	N	N	Shelf	nd	nd	Rare	H					L	L	L	L	L						
Notoraja sp A	Blue skate	*Rajidae*	Y	Y	Y	Y	Mid-slope	200–599	<1	Rare	H					M	L	L	L	L						
Pavoraja nitida	Peacock skate	*Rajidae*	Y	Y	Y	Y	Shelf	<200	69	Common	L	No trend		0.873	L	L	L	L	L	L					3.53	L
Myliobatiformes	Eagle & devil rays, stingrays & stingarees																									
Dasyatis brevicaudata	Smooth Stingray	*Dasyatididae*	Y	Y	Y	Y	Shelf	<200	89	Common	L	No trend		2.123	L	L	L	L	L	L					4.19	M
Dasyatis thetidis	Black Stingray	*Dasyatididae*	Y	Y	Y	Y	Shelf	<200	96	Common	L	No trend		2.232	L	L	L	L	L	L						
Myliobatis australis	Southern eagle ray	*Myliobatidae*	Y	Y	Y	Y	Shelf	<200	88	Abundant	L	No trend		2.077	L	L	L	L	L	L	32	H		H	3.25	L
Trygonoptera mucosa	Western shovelnose stingaree	*Urolophidae*	Y	N	N	N	Shelf	<200	2	Common	L					L	L	L	L	L	17	M			3.50	L
Trygonoptera testacea	Common stingaree	*Urolophidae*	N	N	N	Y	Shelf	<200	31	Common	L	Indeterminable				L	L	L	L	L	13	M		M		
Trygonoptera sp B	Eastern shovelnose stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	<200	<1	Common	L					L	L	L	L	L					3.50	L
Urolophus bucculentus	Sandyback stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	<200	124	Common	L	No trend		0.405	M	L	L	L	L	L	17	H		H	3.59	L
Urolophus cruciatus	Banded stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	<200	70	Common	L	No trend		0.861	L	L	L	L	L	L	10	M		M	3.50	L
Urolophus expansus	Wide stingaree	*Urolophidae*	Y	N	N	N	Upper slope	<200	351	Abundant	L	No trend		1.067	L	M	L	L	L	L					3.52	L
Urolophus gigas	Spotted stingaree	*Urolophidae*	Y	Y	Y	N	Shelf	<200	3	Sparse	M					L	L	L	L	L					3.69	L
Urolophus kapalensis	Kapala stingaree	*Urolophidae*	N	N	N	Y	Shelf	<200	1	Sparse	M					L	L	L	L	L	9	M		M		
Urolophus ovarius	Coastal stingaree	*Urolophidae*	Y	N	N	N	Shelf	nd	nd	Sparse	M					L	L	L	L	L						
Urolophus paucimaculatus	Sparsely-spotted stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	<200	90	Abundant	L	Decreasing		0.615	M	L	L	L	L	L	9	M		M	3.55	L
Urolophus sufflavus	Yellowback stingaree	*Urolophidae*	N	N	N	Y	Shelf	<200	5	Sparse	M					L	L	L	L	L						
Urolophus viridis	Green-backed stingaree	*Urolophidae*	Y	Y	Y	Y	Shelf	<200	455	Abundant	L	Decreasing		0.337	M	L	L	L	L	L	10	M		M	3.53	L
Rhinobatiformes	Shovelnose and guitar rays																									
Aptychotrema rostrata	Eastern shovelnose ray	*Rhinobatidae*	N	N	N	Y	Shelf	<200	23	Common	L	Increasing		9.555	L	M	L	L	L	L					3.59	L
Aptychotrema vincentiana	Western shovelnose ray	*Rhinobatidae*	Y	Y	N	N	Shelf	<200	7	Sparse	M					L	L	L	L	L						
Trygonorrhina fasciata	Southern fiddler ray	*Rhinobatidae*	Y	Y	Y	N	Shelf	<200	219	Abundant	L	Decreasing		1.252	L	L	L	L	L	L					3.66	L
Trygonorrhina sp A	Eastern fiddler ray	*Rhinobatidae*	N	N	N	Y	Shelf	<200	<1	Rare	H					M	L	L	L	L						
Torpediniformes	Electric rays																									
Hypnos monopterygium	Coffin ray	*Hypnidae*	Y	N	N	Y	Shelf	<200	9	Sparse						M	L	L	L	L						
Narcine tasmaniensis	Tasmanian numbfish	*Narcinidae*	Y	Y	Y	Y	Upper slope	<200	56	Common	L	Increasing		4.715	L	M	L	L	L	L					3.50	L
Torpedo macneilli	Short-tail torpedo ray	*Narcinidae*	Y	Y	Y	Y	Upper slope	200–599	72	Common	L	No trend		1.067	L	M	L	L	L	L					4.23	M
Holocephaliformes	Chimaeras																									
Callorhinchus milii	Elephant fish	*Callorhinchidae*	Y	Y	Y	Y	Shelf	<200	48	Abundant	L	Indeterminable				L	H	L	L	L	23	H		H	3.83	L
Chimaera lignaria	Giant chimaera	*Callorhinchidae*	N	N	Y	N	Mid-slope	≥600	<1	Rare	H					H	L	L	L	L	43	H		H	3.66	L
Chimaera sp A	Southern chimaera	*Chimaeridae*	Y	Y	Y	Y	Upper slope	200–599	12	Sparse	M	No trend		0.204	H	H	L	L	M	L	36	H		H	3.68	L
Hydrolagus lemures	Blackfin ghostshark	*Chimaeridae*	Y	Y	N	Y	Upper slope	200–599	11	Sparse	M	No trend		1.274	L	H	L	L	M	L					3.91	L
Hydrolagus ogilbyi	Ogilbys ghostshark	*Chimaeridae*	Y	Y	Y	Y	Upper slope	200–599	10	Sparse	M	No trend		1.870	L	H	L	L	M	L	41	H		H	4.00	M
Hydrolagus sp A	Black ghostshark	*Chimaeridae*	N	Y	Y	Y	Mid-slope	≥600	<1	Rare	H					H	L	L	L	L					3.63	L
Hydrolagus sp C	Giant ghostshark	*Chimaeridae*	N	N	N	Y	Mid-slope	nd	nd	Rare	H					H	L	L	L	L					4.00	L
Harriotta raleighana	Bigspine spookfish	*Rhinochimaeridae*	Y	Y	Y	Y	Mid-slope	≥600	<1	Rare	H					H	L	L	L	L						
Rhinochimaera pacifica	Pacific spookfish	*Rhinochimaeridae*	Y	Y	Y	Y	Mid-slope	≥600	1	Rare	H					H	L	L	L	L	31	H		H	3.95	L

[A]Common before fishing;[B]Abundant before fishing;[C]Historically H (high) when targeted.

Appendix 1: Intellectual Property

No intellectual property has arisen from the research that is likely to lead to significant commercial benefits, patents or licences. Intellectual property associated with information produced from the project will be shared equally by the Fisheries Research and Development Corporation and by the Victorian Department of Primary Industries.

Appendix 2: Staff

The following staff were engaged part-time on the project.

Terry Walker, MAFFRI, Queenscliff, Principal Investigator, supervise work in NSW, Vic, and SA (25%, 3 y).
John Stevens, CSIRO Marine Research, Hobart, Co-Investigator, supervise work in Tas (10%, 3 y).
John Salini, CSIRO Marine Research, Cleveland, Co-Investigator, align with northern project (5%, 3 y)
(Took over from Ilona Stobutzki and Steve Blaber as the Principal Investigator of the northern project).
Peter Last, CSIRO Marine Research, Hobart, Co-Investigator, Taxonomy (10%, 3 y).
Ross Daley, CSIRO Marine Research, Hobart, coordinate laboratory and field activities in Tas (50%, 3 y).
Sharron Appleyard, CSIRO Marine Research, Hobart, molecular genetics (5%, 3y).
Megan Storie, MAFFRI, Queenscliff, coordinate laboratory activities in NSW, Vic, & SA samples (40% 1 y).
Ken Smith, MAFFRI, Queenscliff, coordinate field collection of samples in NSW, Vic, & SA (5% 1 yr).
David McKeown, MAFFRI, Queenscliff, coordinate field collection of samples in NSW, Vic, & SA (5% 1 y).
Corey Green, MAFFRI, Queenscliff, advise and undertake ageing of chondrichthyans (5%, 1 y).
Anne Gason, MAFFRI, Queenscliff, provide statistical and data management support (5%, 3 y).
Masaaki Machida, MAFFRI, Queenscliff, develop and maintain ACCESS databases (15%, 3 y).

The following 11 postgraduate students (10 PhD and 4 BSc (Hons) degrees) are undertaking studies of chondrichthyan species under the project supervision of Terry Walker or John Stevens.

Cynthia Awruck, University of Tasmania, PhD student (3 years 2002/03–2004/05) (complete).
Justin Bell, Deakin University, BSc (Hons) student (1 year 2003), PhD (3 years 2004–06) (incomplete).
Matias Braccini, University of Adelaide, PhD student (3 years 2002/03–2004/05) (complete).
Charlie Huveneers, Macquarie University, PhD student (3 years 2003/04–2005/06) (complete).
Sarah Irvine, Deakin University, PhD student (3 years 2001/02–2003/04) (complete).
David Mossop, Melbourne University, BSc (Hons) student (1 year 2004) (complete).
David Phillips, Deakin University, BSc (Hons) student (1 year 2003/04), PhD (3 years 2005–07) (incomplete).
Matthew Reardon, University of Melbourne, PhD student (3 years 2002/03–2004/05) (incomplete).
Javier Tovar-Ávila, University of Melbourne, PhD student (3 years 2002/03–2004/05) (complete).
Michelle Treloar, Deakin University, PhD student (3 years 2002/03–2004/05) (incomplete).
Fabian Trinnie, Deakin University, BSc (Hons) student (1 year 2002/03), PhD (3 years 2004–06) (incomplete).
Lorenz Frick, Monash University, PhD (3 years 2005/06–2007/08) (incomplete).

Professor William C. Hamlett of the Medical School of the University of Indiana, USA, through ongoing collaborative arrangements with the Principal Investigator, provided supervision of Australian-based postgraduate students working on the project and advice on chondrichthyan reproduction.

Appendix 3. Extension Strategy

Objectives

1. Disseminate a summary and the final report of the findings from the present project to industry and government agencies with responsibilities for management of fisheries and the environment.

2. Provide a comprehensive overview of the relative ecological risks to chondrichthyan species impacted by the effects of fishing in south-eastern Australia to the national Shark Assessment Group (SAG), or the SAG's successor, to assist that body monitor progress on implementation and, if necessary, revise the Shark Plan.

3. Make data on chondrichthyans available as required to researchers undertaking broad ecological risk assessments of the effects of fishing on all Commonwealth managed fisheries as part of a national AFMA funded project led by CSIRO Marine Research.

4. Make data on chondrichthyans available to SharkFAG which provides assessment advice to the MACs associated with the Gillnet Hook and Trap Fishery (GNTF), South East Trawl Fishery (SETF), and Great Australia Bight Trawl Fishery (GABTF).

5. Make data on chondrichthyans available as required to researchers undertaking South-eastern Australian Fisheries Management Options Project funded by FRDC, AFMA, MAFFRI and NOO and led by AFMA.

Target Audiences

1. Shark Assessment Group, which served briefly as an interim steering committee, and the Shark Assessment Group's successor the Shark Implementation Committee, which has been established to monitor progress on implementation of the Shark Plan.

2. Fisheries and environmental management agencies of south-eastern Australia.

3. Fishing industry members and other stakeholders associated with the Southern and Eastern Scalefish and Shark Fishery (SESSF).

4. SharkFAG, which has recently had its responsibilities extended to include assessment of target, byproduct, and bycatch species in the SESSF.

Key Messages

1. Shark and other chondrichthyan species tend to have low biological productivity compared with scalefish and invertebrate species.

2. Biological productivity varies widely among chondrichthyan species and some species require special fisheries management attention or special protection.

3. Data outputs from the project are essential inputs for implementation and subsequent revisions of Australia's National Plan of Action for the Conservation and Management of Sharks developed in response to Australia's international obligation to improve management of its chondrichthyan species.

4. The present project will provide essential information for determining the ecological risk of each chondrichthyan species impacted by fisheries in south-eastern Australia.

5. Data outputs from the project have relevance to all fisheries and environmental management agencies in

south-eastern Australia.

Methods

1. Issue a media release at start of project.

2. Milestone reports and final report made available to appropriate fisheries and environmental agencies, MACs, industry councils, SAG, or SAG's successor, and SharkFAG members as they become available.

3. Verbal reports provided at SAG and SharkRAG meetings.

4. Data on chondrichthyans made available as required to project teams requiring information on chondrichthyan species. Notably this includes the ecological risk assessment of the effects of fishing on all Commonwealth managed fisheries as part of a national AFMA funded project led by CSIRO, and the South-eastern fisheries management options for south-eastern Australia project.

5. Face to face communications with industry members.

6. Staff members of Seanet agreed to participate in dissemination of information to industry.

7. Presentations at scientific conferences, meetings and workshops.

8. Publication in reports and scientific journals.

Action Plan

During Project

Method	Responsibility	Completion date
Press release issued	Principal investigator	15/7/2003
All milestones presented to FRDC, SAG and SharkFAG (SharkFAG will refer to MACs associated with the SESSF).	Principal investigator	6-monthly – 31/5/2005
Presentation of results to SIRC.	Principal investigator	Annually – 31/6/2005
Presentation of results to SharkFAG.	Principal investigator and collaborators	6-monthly – 31/6/2005
Presentation of results at scientific conferences.	Principal investigator and collaborators	Periodically
Publication of results in scientific journals.	Principal investigator and collaborators	Periodically
Presentation to projects addressing ecological risk assessment and projects addressing management options in south-eastern Australia.	Principal investigator	Periodically as required

After Project

Method	Responsibility	Completion date
Final report distributed to all key stakeholders.	Principal investigator	Within 3 months of project completion – 31/12/2005
Presentation of results at scientific conferences and scientific journals	Principal investigator and collaborators	Continue until complete

Evaluation

1. Stakeholders identified above advised of developments.

2. Milestone reports distributed to FRDC, SIRC and SharkFAG.

3. Final report distributed to key stakeholders.

4. Data sets applied for Commonwealth ecological risk assessment.

5. Results appropriately communicated to SIRC in a form where the SIRC can make informed judgements of ecological risks to the chondrichthyan species studied.

6. Results communicated to industry, managers and scientific community.

Appendix 4. Press Release

Rapid assessment of sustainability for ecological risk of sharks & other chondrichthyan bycatch species taken in the GHATF, SETF, and GABTF.

Principal researcher: Terry Walker
Collaborating researcher: John Stevens, CSIRO, Hobart
Collaborating researcher: Steve Blaber, CSIRO, Cleveland

This current 3-year study is funded by the Fisheries Research and Development Corporation (FRDC) and involves close collaboration of researchers from various research establishments. The Marine and Freshwater Resources Institute is leading the study with support from CSIRO and several universities (University of Melbourne, Deakin University, University of Adelaide, University of Hobart, and the University of Indiana).

In Australia, several initiatives taken in recent years have created a requirement to evaluate catch composition and catch rates in Australian fisheries. Fisheries managed under Commonwealth jurisdiction and fisheries producing products for export have to be 'strategically assessed'. This process involves assessing each fishery for ecological impacts on (a) target and by-product species, (b) bycatch species, (c) threatened, endangered and protected species, (d) marine habitats, and (e) marine communities. The process requires collection of appropriate data, risk assessment, and appropriate management responses. High priority is being given to the development of methods that can be applied across species, communities and ecosystems for all Australian fisheries to enable a coordinated and comprehensive assessment strategy. Such an approach must be scientifically defensible, but also pragmatic by being quickly applicable across a wide range of fisheries with varying availability of data.

At a world level, concern for the condition of the stocks of shark and other chondrichthyan species led to the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks), developed recently by the Food and Agriculture Organisation of the United Nations. The IPOA-Sharks recognises that the life-history characteristics of chondrichthyan species (jawed cartilaginous fishes) can make for low 'biological productivity' and cause these animals to be generally more susceptible to overexploitation from fishing than teleost and invertebrate species. The IPOA-Sharks also recognises that these species require special management, research, and monitoring if they are to be harvested sustainably. As a signatory to the IPOA-Sharks, Australia has developed a National Plan of Action for the Conservation and Management of Shark (NPOA-Sharks) which is in the final stages of ratification by all Australian Ministers responsible for fisheries.

In response to the NPOA-Sharks, FRDC is funding the present project and a similar project in northern Australia for the next three years. These two projects are closely aligned with each other to provide appropriate data for ecological risk assessment of the chondrichthyan species of Australia.

For south-eastern Australia, each of more than 100 chondrichthyan species will be graded 'low', 'medium', or 'high' for each of three biological factors. These factors are 'biological productivity' determined from demographic parameters; 'catch susceptibility' determined from approximate measures of 'availability', 'vulnerability', 'gear selectivity', and 'post capture mortality'; and 'relative abundance tends' determined from survey, observations aboard fishing vessels, and fishers' catch-effort reports.

'Biological productivity' relates to the reproductive rate, which increases population size, and to the natural mortality rate, which decreases population size. The reproductive rate is being determined from the proportion of animals in the population breeding each year and from the number of young produced at each pregnancy for viviparous species or the number of eggs laid each year for oviparous species. The natural mortality rate is being estimated from maximum age of animals. Information to help better understand marine food chains and for input into ecosystem models will be provided through analysis of stomach contents. Estimates of bycatch in the major fisheries of southern Australia and abundance trends and distribution are also being made. High abundance species, which are important in terms of ecosystem structure and function, will be investigated more intensively than the less abundant species. The mix of this information will be used for ascribing risk to each species.

Information from the study will be made available to Commonwealth and State agencies with responsibilities relating to management of fisheries, to the fishing industry, and to various scientific working groups involving scientists, members of the fishing industry, fishery managers, and representatives for other stakeholders. In addition to 'strategic assessment', the information will be used for ecological risk assessment, updating of the NPOA-Sharks, updating Bycatch Action Plans, and setting Total Allowable Catches for some byproduct species.

Although the work of this study is centred in the waters off South Australia, Victoria, Tasmania, and NSW, several steps have been taken to ensure that the study addresses national priorities and that the study is closely aligned with a similar FRDC funded study covering the northern half of Australia. One step has been to have the national Shark Assessment Group, which developed the NPOA-Sharks, serve as a steering committee for the project. Another step has been for the Principal Investigator Terry Walker to serve as Co-Investigator on the northern study and for the Principal Investigator Steve Blaber of the northern study serve as a Co-Investigator on the southern-eastern study.

For more information about this project, contact Terry Walker at MAFFRI on 5258 0111.

Appendix 5. Data management and analysis

The success of the rapid assessment method applied as part of the present FRDC project depends on new biological data collected as part of the project and on existing biological data, logbook data, and on-board and in-port monitoring data collected as part of earlier FRDC projects and AFMA projects. This wide range of data and its associated management system are held at the MAFFRI Queenscliff Centre and is referred to as the Southern and Eastern Scalefish and Shark Data Integration Management Summary and Analysis System (SESSF-DIMSAS).

SESSF-DIMSAS is the result of bringing together and integrating separate systems developed for the former Southern Shark Fishery, the former South East Non Trawl Fishery, the South East Trawl Fishery, and the Great Australian Bight Trawl Fishery. The data managed in this system are diverse and complex and the primary data sets are sourced from a wide range of databases. Copies of the primary data are integrated using the data management facilities of SAS to produce secondary data files that can be processed using the data summary and high-level statistical analysis procedures of SAS. The data can also be exported to other MAFFRI systems, other research providers, other agencies acting on behalf of AFMA, and other stakeholders approved by AFMA.

Primary data from logbooks are sourced from isolated databases maintained by AFMA and the State fisheries agencies of Victoria, Tasmania, South Australia, and New South Wales. Primary data from on-board observers, in-port sampling, and laboratory ageing in the Central Ageing Facility are managed in Microsoft ACCESS databases. Similarly, shark tag data collected by all agencies are held in an MS ACCESS database and all biological data on sharks and other chondrichthyans collected by MAFFRI are managed in MS ACCESS databases. The source databases are continually updated and data are edited following data verification and data validation.

SESSF-DIMSAS provides data validation feedback to the collectors of data; it does not alter primary data. SESSF-DIMSAS creates a range of intermediary files between the primary data and the secondary data that allow, where there is good reason, for appropriate correction or suppression of data, which flow through to the secondary data files. Whereas SESSF-DIMSAS does not alter primary data files, intermediary files allow for modification, and documentation of the modification, to secondary data files.

Various components of SESSF-DIMSAS are presented in three figures. Figure 1 shows the system for the former Southern Shark Fishery and chondrichthyan biological data. Figure 2 shows the broad integration of SESSF data. Figure 3 shows the system for the chondrichthyan biological data.

Figure 1. Data integration, management, summary and analysis system for former Southern Shark Fishery and Chondrichthyan Biology

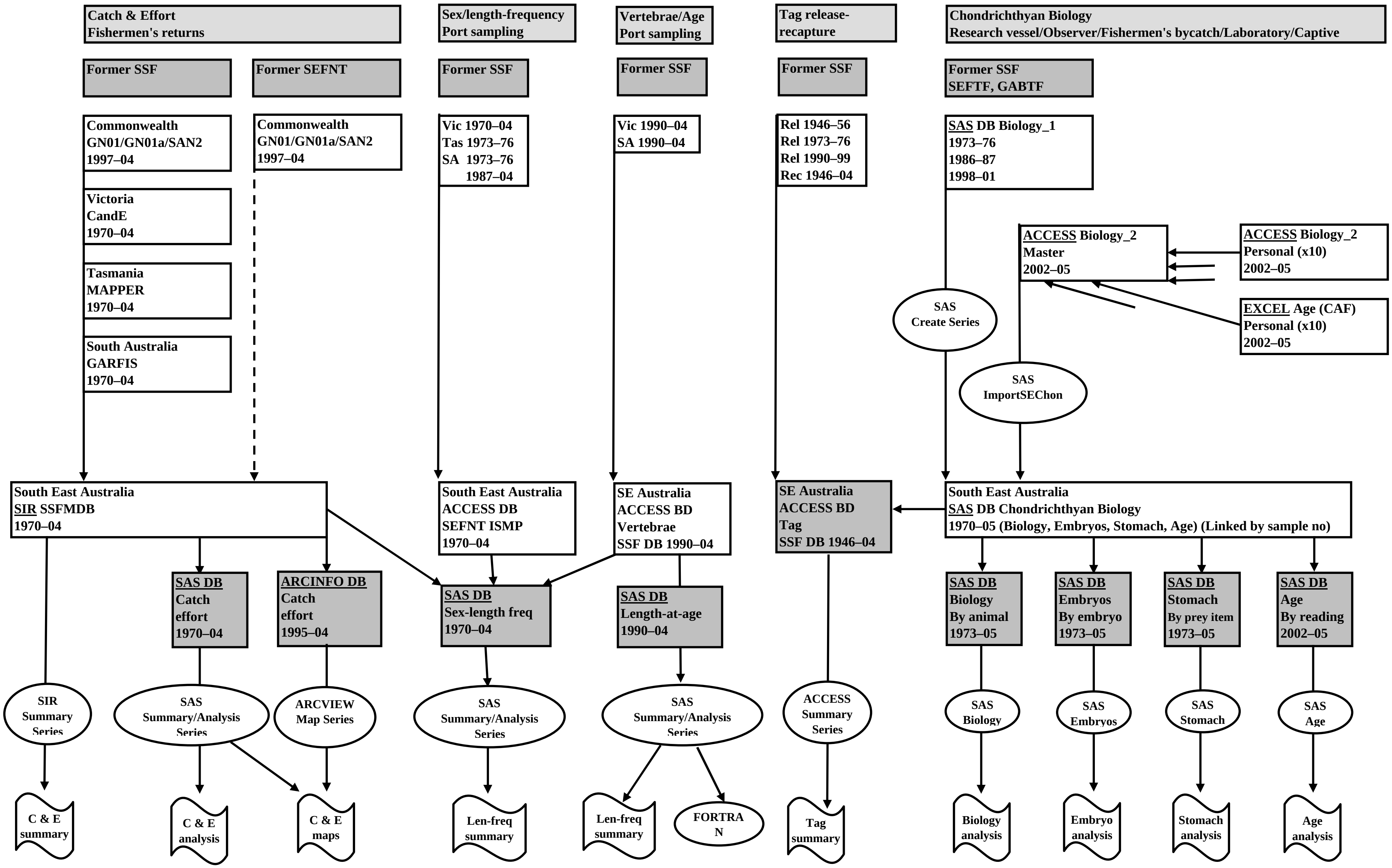


Figure 2. Southern and Eastern Scalefish and Shark Fishery Data Integration, Management, Summary and Analysis System (SESSF-

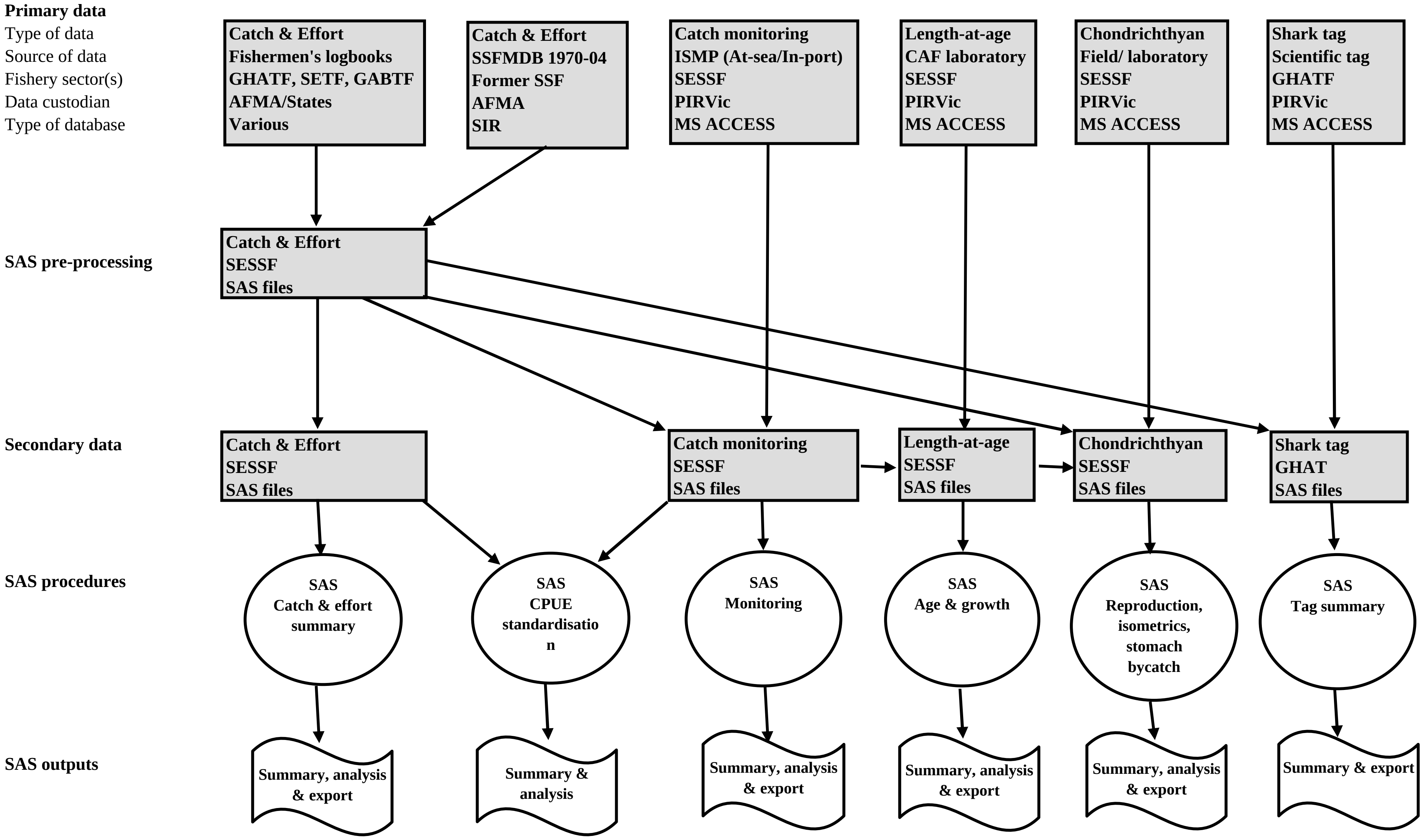
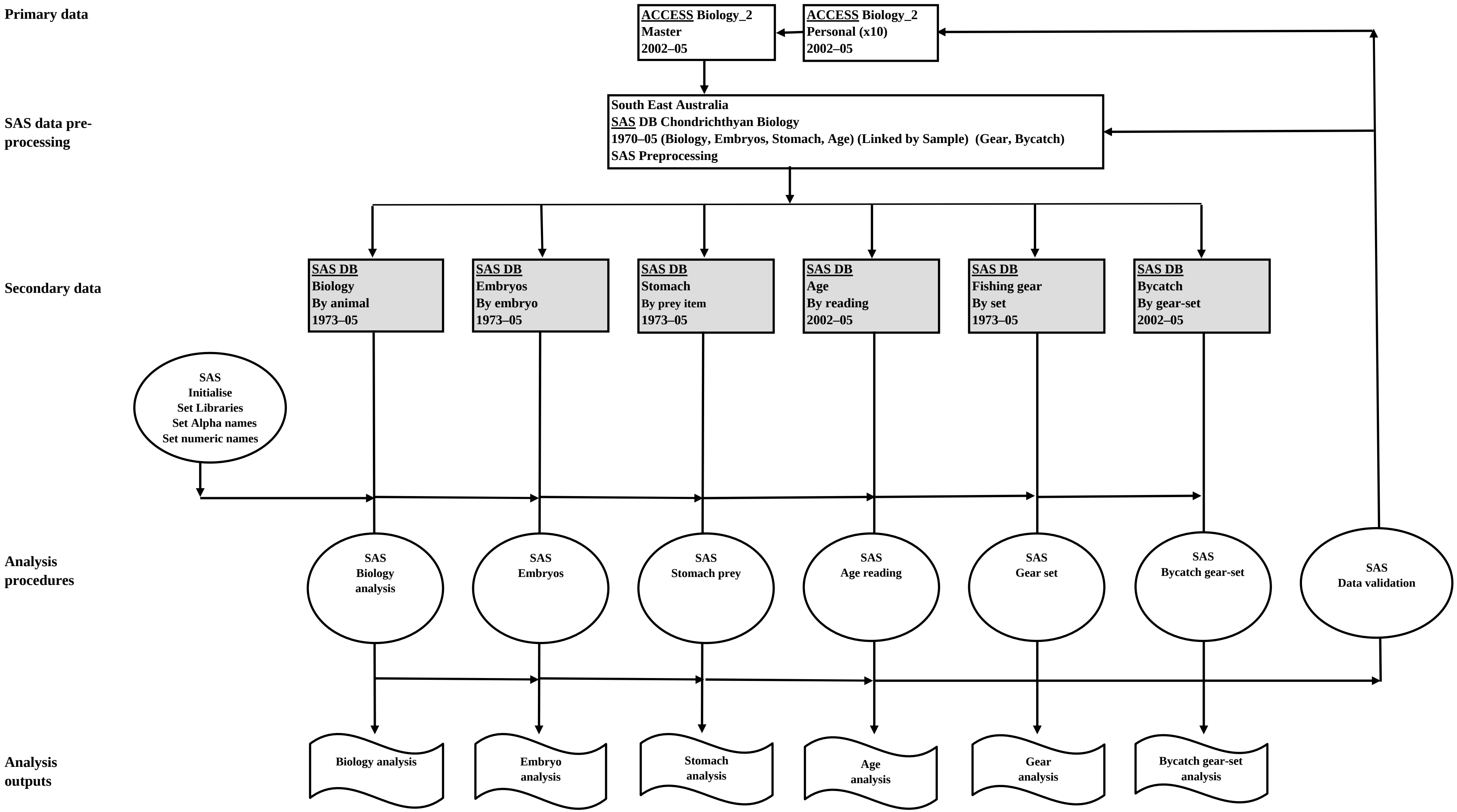


Figure 3. Data integration, management, summary and analysis system for chondrichthyan biological data (Chondrichthyan-DIMSAS)



Appendix 6: Project outputs

A major component of the work contributing to the present project has been published or is in the process of being published. This includes 13 papers published, 2 papers in press, and 2 papers submitted in internationally peer reviewed journals, 4 chapters published in peer reviewed books, and 14 university theses (6 Ph.D and 8 B.Sc. (Hons)). There are presently a further 6 Ph.D. theses in preparation by J. D. Bell, L. Frick, D. T. Phillips, M. B. Reardon, M. A. Treloar, and F. T. Trinnie.

In addition, there have been 39 presentations to scientific conferences, symposia and workshops, 10 seminars or public lectures, 16 presentations to management, industry, or scientific workshops, and 7 documents prepared for SharkRAG.

Scientific papers published (14)

Braccini, J. M., Gillanders, B. M., and Walker, T. I. (2005). Sources of variation in the feeding ecology of the piked spurdog (*Squalus megalops*): implications for inferring predator–prey interactions from overall dietary composition. *ICES Journal of Marine Science* **62**, 1076–1094.

Braccini, J. M., Gillanders, B. M., and Walker, T. I. (2006). Determining reproductive parameters for population assessments of chondrichthyan species with asynchronous ovulation and parturition: piked spurdog (*Squalus megalops*) as a case study. *Marine and Freshwater Research* **57**, 105–119.

Braccini, J. M., Gillanders, B. M., and Walker, T. I. (2006). Total and partial length–length, mass–mass and mass–length relationships for the piked spurdog (*Squalus megalops*) in south-eastern Australia. *Fisheries Research* **78**, 385–389.

Braccini, J. M., Gillanders, B. M., and Walker, T. I. (2006). Hierarchal approach to the assessment of fishing effects on non-target chondrichthyans: case study of *Squalus megalops* in south-eastern Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2456–2466.

Braccini, J. M., Gillanders, B. M. and Walker, T. I. (2006). Notes on population structure of the piked spurdog (*Squalus megalops*) in southeastern Australia. *Ciencias Marinas* **32**, 705–712.

Braccini, J. M., Hamlett, W. C., Gillanders, B. M., and Walker, T. I. (2007). Embryo development and maternal–embryo nutritional relationships of piked spurdog (*Squalus megalops*): maternal contribution or embryonic independence? *Marine Biology* **150**, 727–739.

Braccini, J. M., Gillanders, B. M., Walker, T. I., and Tovar-Ávila, J. (2007). Comparison of deterministic growth models fitted to length-at-age data of the piked spurdog (*Squalus megalops*) in south-eastern Australia. *Marine and Freshwater Research* **58**, 24–33.

Huveneers, C. (2006). Redescription of two species of wobbegong (Chondrichthyes: Orectolobidae) with elevation of *Orectolobus halei* Whitley 1940 to species level. *Zootaxa* **1284**, 29–51.

Huveneers, C., Harcourt, R. G., and Otway, N. M. (2006). Observations of localised movements and residence times of the wobbegong shark *Orectolobus halei* at Fish Rock, NSW, Australia.

Huveneers, C., Otway, N. M., and Harcourt, R. G. (2007). Morphometric relationships and catch composition of wobbegong sharks (Chondrichthyes: *Orectolobus*) commercially fished in New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* **128**, 243–249.

Huveneers, C., Walker, T. I., Otway, N. M., and Harcourt, R. G. (2007). Reproductive synchrony of three

sympatric species of wobbegong shark (genus *Orectolobus*) in New South wales, Australia. *Marine and Freshwater Research* **58**, 765–777.

Irvine, S. B. (2006). Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroselachus crepidator*. *Canadian Journal of Fisheries and Aquatic Science* **63**, 617–627.

Tovar-Ávila, J., Walker, T. I., and Day, R. W. (2007). Reproduction of the Port Jackson shark (*Heterodontus portusjacksoni*) in Victoria, Australia: evidence for two populations and reproductive parameters for eastern population. *Marine and Freshwater Research* **58**, 956–965.

Treloar, M. A., Laurenson, L. J. B., and Stevens, J. D. (2007). Dietary comparisons of six skate species (Rajidae) in south-eastern Australian waters. *Environmental Biology of Fish* **80**, 181–196.

Walker, T. I. (2007). Spatial and temporal variation in the reproductive biology of gummy shark (*Mustelus antarcticus* (Chondrichthyes: Triakidae) harvested off southern Australia. *Marine and Freshwater Research* **58**, 67–97.

Scientific papers in press (1)

Tovar-Ávila, J., Izzo, C. J. F., Walker, T. I., Braccini, J. M., and Day, R. W. (in press). A revised model of dorsal-fin spines growth for chondrichthyan species. *Canadian Journal of Fisheries and Aquatic Sciences* **00**, 00–00.

Scientific papers submitted (3)

Braccini, J. M. (submitted). Weak trophic link among top-predatory sevengill shark species in south-eastern Australia. *Marine and Freshwater Research*, 00, 00–00.

Storrie, M. T., Walker, T. I., Laurenson, L. J., and Hamlett, W. C. (submitted). Microscopic organisation of the sperm storage tubules I the oviducal gland of the female gummy shark (*Mustelus antarcticus*), with observations on sperm distribution and storage. **00**, 00–00.

Tovar-Ávila, J., Troynikov, V. S. Walker, T. I., and Day, R. W. (submitted). Use of stochastic models to estimate the growth of *Heterodontus portusjacksoni* off eastern Victoria, Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **00**, 00–00.

Book chapters (4)

Hamlett, W. C., Kormanik, G., Storrie, M. T., Stevens, B., and Walker, T. I. (2005). Chapter 13. Chondrichthyan parity, lecithotrophy and matrotrophy. pp 395–434. In 'Reproductive biology and phylogeny of Chondrichthyes: sharks, batoids, and chimaeras'. Ed. W. C. Hamlett. 562 pp. (Science Publishers, Inc.: Enfield, New Hampshire 03478, USA.)

Jones, C. C. P., Walker, T. I., Bell, J. D., Reardon, M. B., Ambrosio, C. E., Almeida, A., and Hamlett, W. C. (2005). Chapter 12. Male genital ducts and copulatory appendages in chondrichthyans. p 361–393. In 'Reproductive biology and phylogeny of Chondrichthyes: sharks, batoids, and chimaeras'. Ed. W. C. Hamlett. 562 pp. (Science Publishers, Inc.: Enfield, New Hampshire, USA.)

Walker, T. I. (2005). 13. Management measures. pp 216–242. In 'Management techniques for elasmobranch fisheries'. (Eds Musick, J. A. and Bonfil, R.). 251 pp. *FAO Fisheries Technical Paper* **474**. (Food and Agriculture Organisation of the United Nations: Rome). Also published by APEC Secretariat: Singapore on the internet: http://www.apec.org/apec/publications/free_downloads/2004.html.

Walker, T. I. (2005). Chapter 4 Reproduction in fisheries science. pp 81–127. In 'Reproductive biology and phylogeny of Chondrichthyes: sharks, batoids, and chimaeras'. Ed. W. C. Hamlett. 562 pp. (Science Publishers, Inc.: Enfield, New Hampshire, USA.)

Theses (16)

Awruck, C. A. (2007). The reproductive biology and movement patterns of the draughtboard shark, (*Cephaloscyllium laticeps*): implications for bycatch management. January 2007. 170 pp. Ph.D. Thesis. School of Aquaculture, University of Tasmania, Hobart, Tasmania, Australia.

Bell, J. D. (in preparation). Age estimation and reproductive biology of Australian holocephalans and the whitefin swellshark. 00 pp. Ph.D thesis, Deakin University, Warrnambool, Victoria, Australia.

Braccini, J. M. (2006). Assessment of ecological risks from effects of fishing to the piked spurdog (*Squalus megalops*) in south-eastern Australia. January 2006. 209 pp. Ph.D. Thesis. School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia, Australia.

Huveneers, C. (2007). The ecology and biology of wobbegong sharks (genus *Orectolobus*) in relation to the commercial fishery in New South Wales, Australia. February 2007. Ph.D. Thesis. 307 pp. Macquarie University, Sydney, New South Wales, Australia.

Irvine, S. B. (2004). Age, growth and reproduction of deepwater dogfishes from southeastern Australia. July 2004. 283 pp. Ph.D. Thesis, Deakin University, Warrnambool, Victoria, Australia.

Mossop, D. J. (2004). A comparison of the ecological risk of commercial fishing to the orange spotted catshark (*Asymbolus rubiginosus*) and the rusty carpet shark (*Parascyllium ferrugineum*) in south-eastern Australia. 49 pp. B.Sc. (Hons) Thesis, University of Melbourne, Parkville, Victoria, Australia.

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Walker, T. I. (2004). Rapid assessment for ecological risk of sharks, rays and chimaeras. 1 January 2004. ½ hour presentation to Victorian Minister for Primary Industries. PIRVic Queenscliff Centre, Queenscliff, Victoria, Australia.

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Walker, T. I. (2003) GHATF Shark Longline Sub-Fishery, Ecological Risk Assessment Level 1. Draft 1. 50 pp. SharkFAG 7–9 May 2003. Hobart, Tasmania, Australia. (Updated 11 December 2003).

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Sources of variation in the feeding ecology of the piked spurdog (*Squalus megalops*): implications for inferring predator–prey interactions from overall dietary composition

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Braccini, J. M., Gillanders, B. M., and Walker, T. I. 2005. Sources of variation in the feeding ecology of the piked spurdog (*Squalus megalops*): implications for inferring predator–prey interactions from overall dietary composition. – ICES Journal of Marine Science, 62: 1076–1094.

Sources of variation in dietary composition were examined in the piked spurdog (*Squalus megalops*). The species is an opportunistic predator that consumes a wide range of prey items. When importance of prey was measured by weight or occurrence, *S. megalops* preyed largely on molluscs and teleosts. However, when number of prey was considered, the main items were crustaceans. A bootstrap analysis showed that considerable variability can be expected in the importance of prey items in the species' overall diet. Regional, seasonal, and ontogenetic differences in dietary composition were found, but there were no differences between mature and immature sharks or between males and females. The spatial and temporal variation in diet exhibited by *S. megalops* and the intrinsic natural variability of the dietary composition of this opportunistic predator suggest that studies that infer predator–prey interactions from overall diet are likely to miss information on the ecological relationships among species and thus account for only part of these interactions.

Keywords: Australia, diet, predator–prey interactions, shark, variation.

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Introduction

The feeding ecology of marine animals has been studied to determine the ecological roles and position of animals within foodwebs and to understand predator–prey interactions (Caddy and Sharp, 1986; Pauly *et al.*, 1998; Cortés, 1999). Interactions among species affect population dynamics and also cause indirect ecological effects (Alonzo *et al.*, 2003). Hence, if interactions among species were determined, ecosystems could be managed with higher certainty (Yodzis, 1994). Traditional single-species fishery management ignores fishery impacts on ecosystems (Agardy, 2000). As an alternative, ecosystem-based fishery management has been proposed to account for such impacts (Gulland, 1978; Caddy and Sharp, 1986; Fulton *et al.*, 2003). Many ecosystem models use dietary information as a proxy for the interactions among species (e.g. Christensen, 1995; Walters *et al.*, 1997; Yodzis, 1998). However, most models use overall diet data, ignoring many sources of variation that can affect the dietary composition of predators.

Natural systems are dynamic and vary in time and space (Paine, 1988). It is, therefore, expected that diet of predators, and hence predator–prey interactions, may also vary in time and space. Trophic interactions are determined by the size of predators and their prey (Floeter and Temming, 2003), but little is known about predator–prey size relationships of large marine predators such as sharks. Also for sharks, the effects of time and space and their interactions with other potential sources of variation in their diet, such as sex or maturity condition, have been little studied. Although some studies have reported regional,

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seasonal, or ontogenetic differences in diet (see Wetherbee and Cortés, 2004, for a review), many studies on the diet of sharks have been limited to simple lists of prey items (Heithaus, 2004). Moreover, variation in diet has often been reported qualitatively with little statistical support (Ferry and Cailliet, 1996; Cortés, 1997; Wetherbee and Cortés, 2004). Hence, a more rigorous and quantitative approach is required to study the feeding ecology of sharks.

The piked spurdog (*Squalus megalops*) is a suitable species to test for the effects of potential sources of variation in the dietary composition of predators, as it is a very abundant shark in southern Australia (Jones, 1985; Bulman *et al.*, 2001; Graham *et al.*, 2001). *S. megalops* inhabits waters of the continental shelf and upper continental slope to 510 m (Last and Stevens, 1994). Off South Africa, females grow larger (782 mm total length, TL) than males (572 mm TL) and attain 50% maturity at 15 years, and 50% of males are mature at 9 years old (Watson and Smale, 1999). Given its high natural abundance, which has remained stable since it was first surveyed (Graham *et al.*, 2001), *S. megalops* is a dominant and ecologically important species (Bulman *et al.*, 2001) that is likely to make an important contribution to the structure and functioning of an ecosystem. Nevertheless, information on its feeding habits is scarce. Its overall diet has been described for animals caught off South Africa and eastern Australia, where it preys mainly on teleosts and cephalopods, but it also consumes crustaceans and elasmobranchs (Bass *et al.*, 1976; Ebert *et al.*, 1992; Bulman *et al.*, 2001). Although those studies offer a preliminary description of the diet of this shark, more quantitative analyses are needed.

The purpose of this study was to investigate the effects of several sources of variation in the feeding ecology of *S. megalops*. The specific objectives were to: (i) quantify its overall dietary composition and account for how much variability would be expected when calculating overall prey importance; (ii) examine relationships between prey and predator size; and (iii) test for the effects of region, maturity condition, sex, season, and ontogenetic variation on its dietary composition.

Material and methods

Sampling

S. megalops were obtained from the bycatch of shark and trawl vessels operating in the Australian southern and eastern scalefish and shark fishery (Figure 1). Samples were collected monthly between October 2002 and April 2004, with the exception of the period July−September (Table 1), when *S. megalops* seems to move off the fishing grounds and weather conditions restricted sampling. The specimens were sexed, measured (TL ±1 mm) and weighed on an electronic balance (±0.1 g). Maturity of males was determined on the basis of clasper calcification, condition of testes and vas efferens, and presence of semen in seminal vesicles. Maturity of females was determined on the basis

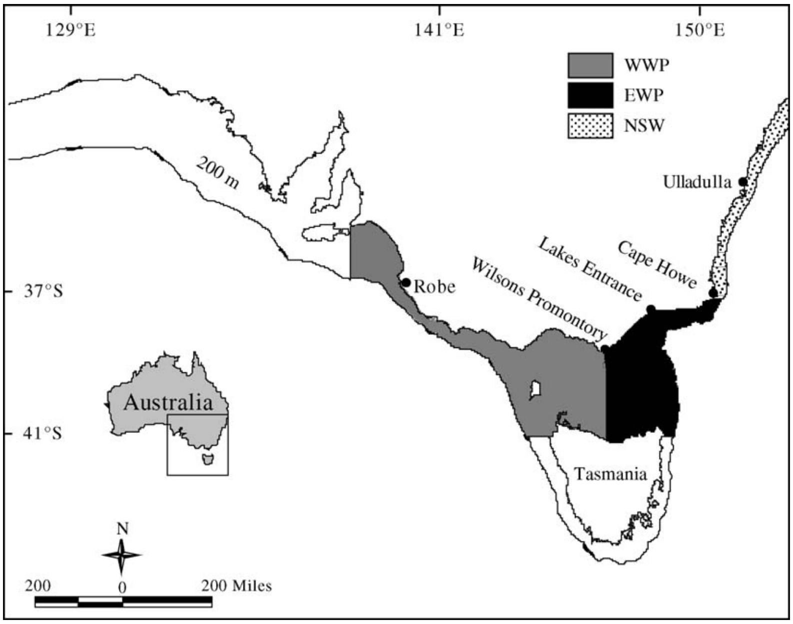

Figure 1. Map of the sampling area showing the three biogeographic regions and ports − west of Wilsons Promontory (WWP); east of Wilsons Promontory (EWP); New South Wales (NSW).

Table 1. Sampling sites (see Figure 1), collection time, and sample sizes collected for the spatial, temporal, ontogenetic, maturity condition, and sexual components of the study (sample sizes for the analyses may be smaller because of the occurrence of empty stomachs).

Factor	Site	Collection time	Sample size
Spatial (large females ≥ 471 mm TL)			
West Wilsons Promontory (WWP)	Robe	Autumn 2004	36
East Wilsons Promontory (EWP)	Lakes Entrance	Autumn 2004	60
New South Wales (NSW)	Ulladulla	Autumn 2004	41
Temporal (seasonal)			
Summer	Lakes Entrance	December 2002, February 2003, 2004	116
Autumn		March 2003, 2004, April, May 2003	98
Winter		June 2003	24
Spring		October 2002, November 2003	71
Size (ontogenetic)[*]			
Small male (≤400 mm TL)	Lakes Entrance	Spring 2002, 2003, Summer 2003, 2004, Autumn 2003, 2004	30
Small female (≤400 mm TL)			51
Medium-sized females (401−470 mm TL)			92
Large male (401−470 mm TL)			37
Large female (≥ 471 mm TL)			100
Maturity condition			
Immature	Lakes Entrance	Spring 2002, 2003, Summer 2003, 2004, Autumn 2003, 2004	174
Mature			131
Sexual			
Male	Lakes Entrance	Spring 2002, 2003, Summer 2003, 2004, Autumn 2003, 2004	67
Female			242

[*] *S. megalops* has a tendency to segregate by sex/size, and this was reflected in the size frequency distribution of some of the fishing shots analysed. Hence, the size classes compared are based on this segregation pattern.

of the condition of oviducal glands and ovarian follicles, and the presence of *in utero* eggs or embryos.

Diet and data analyses

Diet was studied by prey identification and analysis of stomach contents. The stomach of each fish was removed, and the contents were identified to the lowest taxon practical. When possible, to correlate size of prey and predator, body width (BW) of worms, TL of fish, mantle length (ML) of cephalopods, and shield length (SL) of hermit crabs were measured to the nearest millimetre. Where these lengths could not be measured, TL of fish, ML of cephalopods, and SL of hermit crabs were estimated from hard tissue pieces found in stomach contents by linear and allometric relationships determined by regression, using a personal reference collection and the fish and crustacean reference collections of the South Australian Museum, Australia, and Museum Victoria, Australia. Prey items that digest more speedily than other prey items or soft-bodied prey may be under-represented if the more persistent hard parts are included in the analyses (Bigg and Fawcett, 1985; Bigg and Perez, 1985). Hence, hard parts (e.g. beaks, vertebrae, chelipeds) were only used for estimating prey item size and describing the overall dietary spectrum, but they were excluded from further analyses.

Taxonomic classification of prey items does not account for differences in habitat utilization of a predator. Therefore, data analyses were carried out by main zoological group (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, Teleostei) and ecological group separately. The ecological groups considered were benthic infauna (prey species living in the sediment), benthic epifauna (prey species living on the sediment surface), benthic (prey species living on the bottom), demersal benthic (prey species living near the bottom but not linked to it), demersal pelagic (prey species with extensive diel vertical migration), and pelagic (prey species living in the upper layers of the water column).

Overall diet

Stomach fullness (SF) and number of prey found in each stomach were recorded to determine the feeding pattern of *S. megalops*. Stomach fullness was recorded using a quarterly scale (0, empty; 1, 0−25% filled; 2, 26−50% filled; 3, 51−75% filled; 4, 76−100% filled). χ^2 tests with Yates' continuity correction (Zar, 1999) were used to test for differences in the distribution of SF.

To obtain a precise description of the overall diet of a predator, it is important to determine the minimum number of stomachs required (Ferry and Cailliet, 1996; Cortés, 1997). The number of *S. megalops* collected was tested to determine whether sufficient sharks were sampled. Items such as sponges, hydroids, and algae were considered incidental, and were excluded from the analysis. The cumulative number of randomly pooled stomachs was plotted against the cumulative diversity of stomach contents. Diversity was calculated using the pooled quadrat method based on the Brillouin Index of diversity (HZ; Pielou, 1966). To ensure that curves reached an asymptotic value, 10 random orders of stomachs (curves) were calculated (Koen Alonso *et al.*, 2002). Diversity curves were considered asymptotic if at least two previous values to the total sample diversity were in the range of asymptotic diversity ±0.05 (Koen Alonso *et al.*, 2002). Diversity curves were calculated for each combination of factors considered in the analyses of variation in dietary composition.

No single method of analysis of stomach contents completely describes the diet of a predator (Hyslop, 1980); hence, the importance of prey items was evaluated using percentage weight (%W), percentage number (%N), percentage frequency of occurrence (%FO), and percentage Index of Relative Importance (%IRI; Pinkas *et al.*, 1971; Cortés, 1997). Bootstrap methods (1000 replicates) were used to estimate confidence intervals (2.5th and 97.5th percentiles) around the dietary parameters (mean %W, %N, %FO, and %IRI; Haddon, 2001). From the original data matrix, random samples of the observations (i.e. each individual stomach) with replacement were generated to obtain the probability distribution of the dietary parameter estimates for each prey item.

Predator−prey size relationship

The relationship between prey size and shark size was determined using the Spearman rank correlation coefficient (r_s). The length variables for the different taxonomic groups were considered. Relative and cumulative frequency histograms of prey size:predator size ratios were plotted to examine the patterns of prey size consumed by *S. megalops* (Bethea *et al.*, 2004). For this latter analysis, only teleost and cephalopod prey were used.

Variation in dietary composition

Regional comparisons of diet were made for large females (471−650 mm TL) collected in autumn (Table 1). A one-way non-parametric multivariate analysis of variance (NP-MANOVA) using Bray−Curtis distances (Anderson, 2001) on weight and number data for sharks collected at the same time (autumn 2004) was used to test for regional effects on the diet of *S. megalops*. Weight and number data were transformed to fourth root and standardized to z-scores to minimize differences attributable to stomach size. Region was treated as a fixed factor. Equal sample sizes were used (n = 30 for the analysis of zoological groups, n = 28 for the analysis of ecological groups). If significant differences were found, *a posteriori* pairwise comparisons were made (Anderson, 2001).

Maturity condition was evaluated, and sexual, seasonal, and ontogenetic comparisons were made on sharks collected from Lakes Entrance between October 2002 and March 2004 (Table 1). Non-parametric multidimensional scaling (nMDS) on Bray−Curtis similarity measures using fourth root transformed data (Clarke, 1993) were used to visualize patterns of variation in dietary composition. Mean percentage weight and number of zoological and ecological groups were used.

The relative and interactive effects of maturity condition, sex, season, and size were evaluated in a similar way to the regional analysis using weight and number. *S. megalops* is sexually dimorphic, females attaining larger size than males; hence, separate analyses were undertaken for each sex to investigate the effects of maturity condition on dietary composition. The effects of maturity condition (mature, immature) and season (summer, autumn, spring; Table 1) were investigated using individuals within the 382−406 and 433−509 mm TL range for males and females, respectively. These ranges covered the sizes of the smallest mature and largest immature specimen of each sex. For the analysis of males, season was not included as a factor because of the low number of replicates for any season except summer. Hence, the analysis was done using data collected only during the latter season. For females, maturity condition was treated as fixed and orthogonal to the random factor season (i.e. every level of the factor "maturity", mature or immature, is present in every level of the factor "season", summer, autumn, or spring; Table 1). Similar sample sizes (n = 7 for males, n = 8 for females) were used for each combination of factors.

To test for sexual, ontogenetic (size), and seasonal differences, sharks of similar size (<471 mm TL) were used in a three-way NP-MANOVA (factors: sex, size, and season). Sex (males, females) and size (small and large males, small and medium-sized females) were treated as fixed and orthogonal to the random factor season (summer, autumn, spring; Table 1). Equal sample sizes (n = 6) were used for each combination of factors. As small and large males and small and medium-sized females had similar diets (see below), data were pooled to test for ontogenetic and seasonal differences between small (<471 mm TL) and large (≥ 471 mm TL) animals. A two-way NP-MANOVA (factors: size and season) with equal sample sizes (n = 26) was used for each combination of factors. Finally, winter samples could only be collected for small specimens, so to include winter in the seasonal study, a one-way NP-MANOVA was undertaken for small *S. megalops* using a balanced design (n = 24).

Results

The stomach contents and fullness of 937 *S. megalops* were examined. In all, there were 77 small males (274–400 mm TL), 105 small females (270–400 mm TL), 129 large males (400–470 mm TL), 193 medium-sized females (401–470 mm TL), and 433 large females (471–650 mm TL).

Overall diet

Of the 937 stomachs examined, 603 (65.3%) contained food, from which >60% contained a single prey item. For stomachs with >1 item, the number of prey items ranged from two to ten. For stomachs with prey, the distribution of stomach fullness was relatively even (~25%) and there were no significant differences among the frequency of individuals in each SF category ($\chi^2 = 2.150$, n = 603, p = 0.542).

Of the 603 stomachs with food, 111 were excluded because they contained only hard parts, sponges, hydroids, algae, or unidentified material. The prey diversity curve for the overall diet reached a stable level at about 350 stomachs (Figure 2a), so the sample size of 492 was large enough to describe the overall diet of *S. megalops*.

The stomachs contained 107 taxonomic levels of prey item: six polychaetes, two sipunculids, 29 crustaceans, 17 molluscs, 47 fish, remains of sea lion, and other items such as echiurids, algae, sponges, hydroids, and brittle stars (Appendix). Arrow squid (family Ommastrephidae) was the dominant prey item, contributing the highest values of %W (20.03%), %N (7.54%), %FO (8.76%), and %IRI (32.05%). Octopus (*Octopus* sp.) was the second most important prey item by weight (12.55%), frequency of occurrence (7.66%), and relative importance (19.37%). The third major prey was fish of the family Triglidae (gurnards) in terms of weight (9.77%), number (5.33%), frequency of occurrence (5.97%), and relative importance (12.00%). Shrimps (Caridea) and hermit crabs (Diogenidae) were important by number (6.88% and 5.90%, respectively), but not in terms of weight or frequency of occurrence.

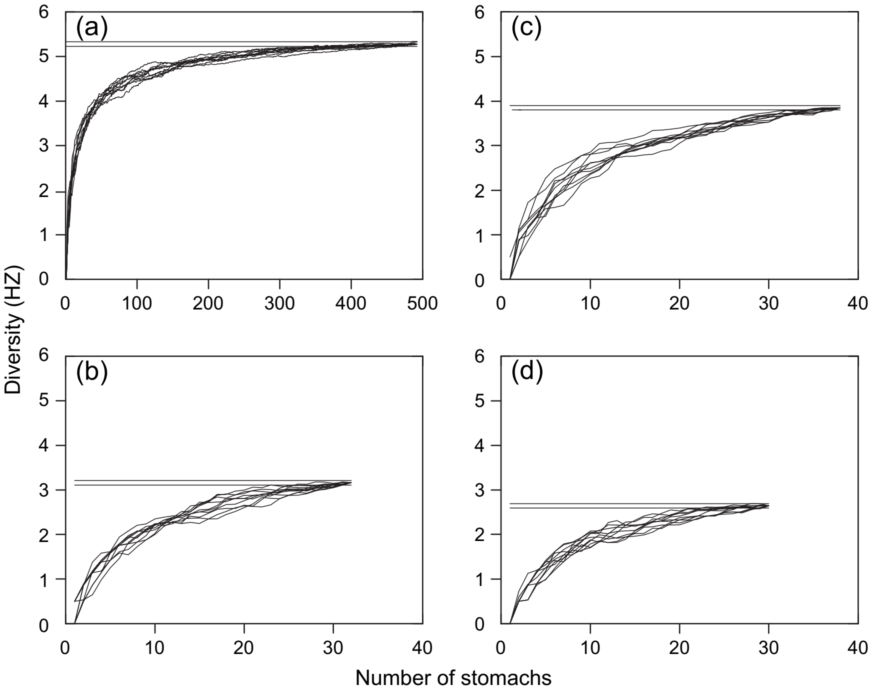

Figure 2. Cumulative diversity (HZ) of prey items for (a) the overall diet of *S. megalops* and for the three regions analysed: (b) west of Wilsons Promontory, (c) east of Wilsons Promontory, (d) New South Wales. The straight lines indicate the range of asymptotic diversity ±0.05.

A similar pattern was observed when data were analysed by main zoological group (Appendix). Molluscs were the most important item by weight (56.43%), frequency of occurrence (35.89%), and relative importance (50.31%). However, the most numerous items were crustaceans (31.61%). Teleosts were the second most important item in terms of weight (38.32%), frequency of occurrence (34.03%), and relative importance (37.27%).

When data were analysed by ecological group, the most important group by weight was demersal pelagic prey (40.25%), followed by benthic (36.95%), and demersal benthic (11.04%) prey (Appendix). In contrast, benthic epifauna dominated by number (41.15%) and frequency of occurrence (29.41%), followed by benthic prey (21.10% by number and 25.35% by frequency of occurrence). Finally, for %IRI, the main ecological group was benthic prey (33.96%), followed by benthic epifauna (30.70%), demersal pelagic (26.52%), and demersal benthic (6.27%) prey. Pelagic and benthic infauna were less important.

Irrespective of analysing prey items by zoological or ecological group, considerable variability was found around the estimation of overall mean prey importance (Appendix). For important prey such as molluscs or teleosts, there was ~20% of variability within the upper and lower 95% confidence intervals. However, for less important prey such as crustaceans, variability was ~50%. When the mean values obtained from bootstrapping were compared with those obtained from point estimates of overall diet, variability ranged from 1 to 14% (not shown). A similar pattern was observed for ecological groups.

Predator—prey size relationship

S. megalops consumed prey of a wide range of sizes (Figure 3). More than 60% of teleosts and cephalopods consumed were less than 30% and 24% of *S. megalops* total length (TL), respectively, but *S. megalops* also consumed fish and cephalopods up to 60% of its TL.

No correlation was found between predator TL and shield length of hermit crabs ($r_s = 0.119$, $n = 65$, $p > 0.05$), TL of teleosts ($r_s = 0.157$, $n = 39$, $p > 0.05$), or body width of worms ($r_s = 0.273$, $n = 14$, $p > 0.05$). However, there was a positive correlation between predator TL and mantle length of cephalopods ($r_s = 0.455$, $n = 43$, $p < 0.05$; Figure 3).

Variation in dietary composition

Prey diversity for sharks collected from WWP (~3.10; Figure 2b) and NSW (~2.64; Figure 2d) was lower than that for sharks from EWP (~3.85; Figure 2c), suggesting a more diverse diet at EWP. The prey diversity curves reached a stable level for each of the three regions analysed, indicating that the sample was large enough to describe the diet of sharks from each region.

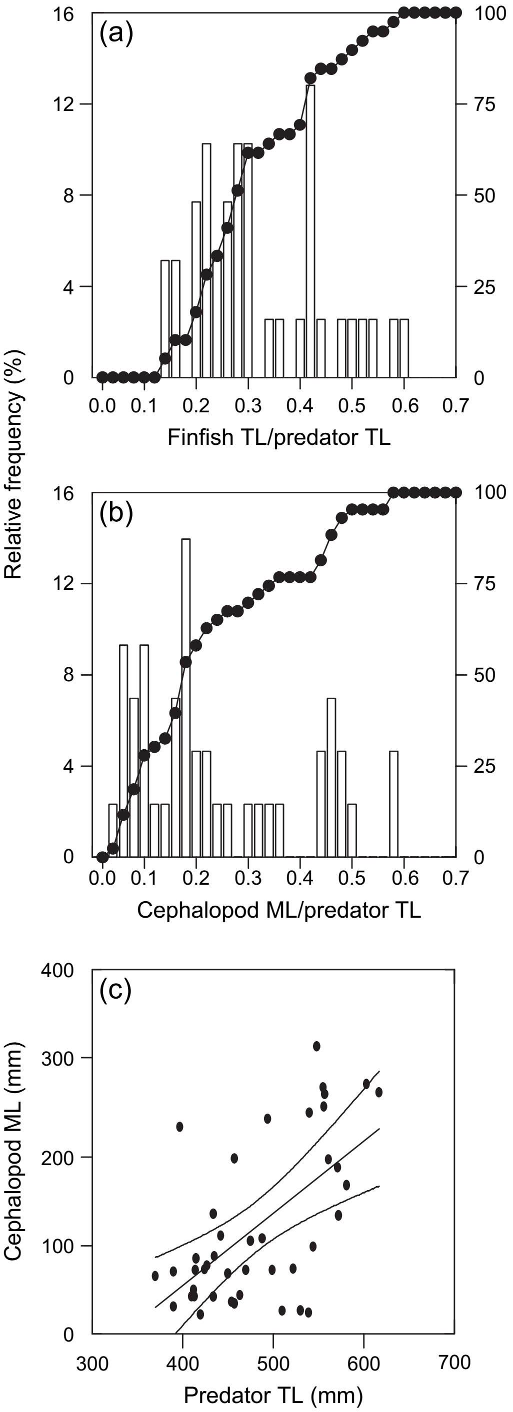

Figure 3. Changes in prey size with predator size. Distribution of prey size:predator size ratios for (a) teleosts and (b) cephalopods. (c) Relationship between cephalopod mantle length (ML) and predator total length (TL) and 95% confidence limits. $ML = 0.6894TL - 218.68$; $r^2 = 0.37$. Open bars = relative frequencies at 0.02 intervals. Filled circles = cumulative frequencies at 0.02 intervals.

There was a regional pattern in the diet of *S. megalops* (Table 2). Significant differences in dietary composition were found between sharks collected from WWP and EWP, irrespective of the use of weight or number of zoological or ecological groups (Figure 4; pairwise comparisons). Significant differences were also found between sharks collected from WWP and NSW when weight of zoological group and weight or number of ecological group were used (Figure 4; pairwise comparisons). No differences were found between the diets of sharks collected from EWP and NSW (Figure 4; pairwise comparisons). For EWP and NSW, *S. megalops* consumed mainly teleosts, molluscs, and crustaceans, and also small amounts of worms and chondrichthyans for EWP. However, for WWP, *S. megalops* preyed largely on molluscs and, to a lesser extent, teleosts. For ecological groups, *S. megalops* collected from WWP preyed mostly on demersal pelagic prey, whereas those collected from EWP and NSW preyed mostly on benthic organisms.

Most prey diversity curves (not shown) showed asymptotes or trends towards an asymptote for each combination of maturity condition and season. Irrespective of the use of weight or number of a zoological or an ecological group, there were no significant differences in dietary composition between immature and mature *S. megalops* (Table 3). Therefore, immature and mature sharks were pooled for subsequent analyses.

Most prey diversity curves (not shown) showed asymptotes or trends towards an asymptote for each combination of sex, size, and season. A significant seasonal pattern in the dietary composition of *S. megalops* was found for the three-way analysis, but there were no sexual or ontogenetic differences (Table 4). Therefore, both sexes and sizes (small and large males, and small and medium-size females) were pooled for subsequent analyses.

Table 2. NP-MANOVA testing for the effects of region (east of Wilsons Promontory, west of Wilsons Promontory, New South Wales) on the weight and number of zoological (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, and pelagic) in the diet of *S. megalops*.

		Weight		Number	
Factor	d.f.	F	p	F	p
Zoological group					
Region	2	4.965	<0.001	3.580	0.011
Residual	87				
Ecological group					
Region	2	6.561	<0.001	6.990	<0.001
Residual	81				

Prey diversity curves for each size−season combination reached a stable level and had similar values of diversity, except for small sharks collected in winter that showed lower values (Figure 5). After including all sizes in the analysis, significant ontogenetic and seasonal effects were detected. Also, a significant interaction between size and season was found for weight and number of prey items for both zoological and ecological groups (Figures 6, 7; Table 4). The ordination showed two separate groups when zoological data and ecological number data were used (Figure 6). Large sharks tended to be separated from small ones, and samples collected in summer and autumn were separated from those collected in spring. However, no clear visual pattern was observed when the analysis was done for ecological groups using weight data. Large and small *S. megalops* had different diets in summer and autumn but similar diets in spring (Figure 7; pairwise comparisons). In summer and autumn, large sharks consumed mainly molluscs, whereas small sharks consumed mainly crustaceans. For ecological groups in summer, large *S. megalops* preyed mainly on demersal pelagic prey whereas small sharks preyed on benthic organisms. In spring, both size classes had a similar feeding pattern, consuming mainly teleosts, followed by molluscs and crustaceans. By ecological group, large and small sharks collected in spring preyed mainly on benthic organisms. When winter was included in the seasonal analyses, the seasonal pattern was similar (Table 5). Dietary composition in summer, autumn, and winter was similar, but significant differences were observed among these three seasons and spring (pairwise comparisons).

Discussion

Dietary studies of sharks commonly report a high proportion of empty stomachs and few prey items per stomach, most of them in advanced stages of digestion (Wetherbee *et al.*, 1990; Ebert *et al.*, 1992; Simpfendorfer *et al.*, 2001a). Therefore, many shark species are considered intermittent feeders. For such species, short periods of active feeding are followed by longer periods of reduced predatory activity (Wetherbee *et al.*, 1990; Wetherbee and Cortés, 2004). The present study supports this hypothesis. Almost 35% of stomachs examined were empty, and for stomachs with prey, >60% contained a single prey item, suggesting that feeding is intermittent. However, further research on the feeding duration, total digestion time, and gastric evacuation rates using captive *S. megalops* would allow estimates of feeding frequency and feeding periodicity.

There was a wide range of food items in the stomachs of *S. megalops*, which meant that many stomachs were needed to describe overall diet. When diversity curves have been used to determine the sample size required for a precise description of the diet of sharks, most studies have found stable levels of diversity at <200 stomachs sampled (Carrassón *et al.*, 1992; Gelsleichter *et al.*, 1999; Koen

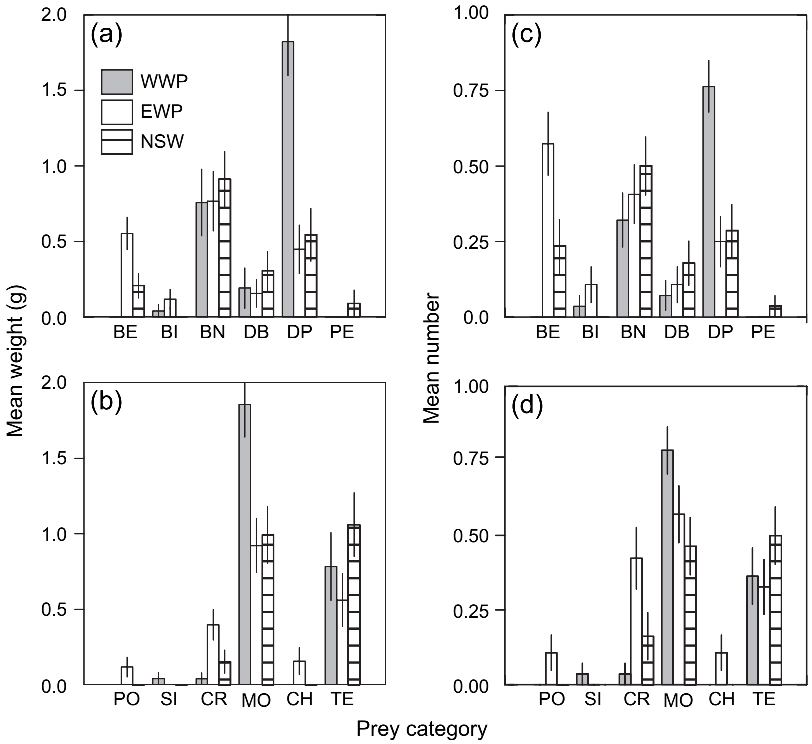

Figure 4. Main prey groups found in the diet of *S. megalops* collected from west of Wilsons Promontory (WWP), east of Wilsons Promontory (EWP), and New South Wales (NSW). Mean weight of fourth root transformed data (±s.e.) of prey sorted by (a) ecological and (b) zoological group, and the mean number of fourth root transformed data (±s.e.) of prey sorted by (c) ecological and (d) zoological group. BE, benthic epifauna; BI, benthic infauna; BN, benthic; DB, demersal benthic; DP, demersal pelagic; PE, pelagic. PO, polychaetes; SI, sipunculids; CR, crustaceans; MO, molluscs; CH, chondrichthyans; TE, teleosts.

Alonso *et al.*, 2002; Morato *et al.*, 2003; Bethea *et al.*, 2004). However, prey diversity was high for *S. megalops*, and at least 350 stomachs had to be sampled to describe its overall diet. *S. megalops* can be considered a generalist and opportunistic feeder given that portions of large teleosts, cephalopods, and sharks were found in many stomachs, and that they consumed abundant prey such as arrow squid (Triantafillos *et al.*, 2004) and gurnards (Triglidae;

Table 3. NP-MANOVA testing for the effects of maturity condition (mature, immature) and season (summer, autumn, spring), females only, on the weight and number of zoological groups (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, and Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, pelagic) in the diet of male and female *S. megalops*.

		Zoological group				Ecological group			
		Weight		Number		Weight		Number	
Factor	d.f.	F	p	F	p	F	p	F	p
Male									
Maturity	1	1.045	0.394	1.094	0.391	0.488	0.730	0.543	0.738
Residual	12								
Female									
Maturity	1	3.122	0.080	3.551	0.080	1.779	0.307	1.742	0.289
Season	2	1.843	0.077	1.800	0.107	1.374	0.190	1.370	0.206
Maturity × season	2	0.559	0.804	0.471	0.827	0.460	0.912	0.385	0.930
Residual	42								

Table 4. NP-MANOVA testing for the effects of sex (male, female), size (small and large for males, small, medium-sized, and large for females), and season (summer, autumn, spring) on the weight and number of zoological (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, pelagic) in the diet of *S. megalops*.

		Zoological group				Ecological group			
		Weight		Number		Weight		Number	
Factor	d.f.	F	p	F	p	F	p	F	p
3-way analysis for sharks < 471 mm TL									
Sex	1	0.505	0.619	0.508	0.602	2.622	0.190	2.764	0.189
Size	1	0.741	0.520	0.667	0.537	3.938	0.120	4.205	0.120
Season	2	5.130	<0.001	5.579	<0.001	3.963	<0.001	4.378	<0.001
Sex × size	1	0.315	0.782	0.211	0.841	1.161	0.390	1.085	0.425
Sex × season	2	0.750	0.582	0.826	0.516	0.583	0.817	0.569	0.804
Size × season	2	1.980	0.077	2.172	0.062	0.565	0.841	0.545	0.840
Sex × size × season	2	2.227	0.051	2.245	0.057	1.660	0.094	1.693	0.098
Residual	60								
2-way analysis for all sizes including large females (≥ 471 mm TL)									
Size	1	4.407	0.059	4.189	0.094	5.157	0.018	6.557	0.017
Season	2	6.935	<0.001	6.983	<0.001	8.978	<0.001	8.220	<0.001
Size × season	2	6.051	<0.001	7.826	<0.001	1.984	0.048	2.495	0.017
Residual	150								

M. Gomon, pers. comm.). Other studies also suggest that sharks are generalist and opportunistic feeders that consume the most abundant prey (Wetherbee *et al.*, 1990; Hanchet, 1991; Ellis *et al.*, 1996; Koen Alonso *et al.*, 2002).

Overall, results differed when average prey importance was analysed using weight, number, or frequency of occurrence of prey groups. If importance of prey is to be deduced on the basis of weight or frequency of occurrence, *S. megalops* preyed largely on molluscs and teleosts. However, if number of prey is to be used, the main items were crustaceans. Analyses done by ecological group showed that *S. megalops* was a versatile predator that used a wide range of habitats. The most important items by weight were demersal pelagic and benthic prey, whereas benthic epifauna and benthic prey were the most consumed items by number and occurrence. Therefore, number, weight, and frequency of occurrence measures provided different information on feeding habit (MacDonald and Green, 1983; Bigg and Perez, 1985; Cortés, 1998). Ferry and Cailliet (1996) suggest using multiple measures when prey items differ in size. For generalist and opportunistic feeders that consume a wide range of prey, like *S. megalops*, the use of multiple measures allows better representation of overall diet.

Irrespective of which diet descriptor was used, the bootstrap analysis showed a wide range of variability around the estimate of overall importance of prey. In general, studies on the diet of sharks obtain samples opportunistically, and in many cases small sample sizes are collected. However, as sharks are considered opportunistic predators (Wetherbee *et al.*, 1990), large sample sizes would be needed for a comprehensive description of diet. Also, many studies have reported a high proportion of empty stomachs (Wetherbee *et al.*, 1990), and some studies only described diet in terms of number or occurrence of prey, whereas other studies used only weight. However, for *S. megalops*, number, occurrence, and weight of prey showed different patterns of importance of prey. Therefore, a combination of small sample size, high proportion of empty stomachs, the use of different descriptors of importance of prey, and the opportunistic predatory nature of many shark species, is likely to result in high variability in the dietary composition and hence in evaluation of predator–prey interactions. Accurate characterization of predator–prey interactions inferred from diet data is crucial for ecosystem-based models and in their increasing use as tools for fisheries management. However, if overall diet data do not incorporate a measure of the natural variability in dietary composition exhibited by many shark species, predatory interactions and hence model predictions may be misleading. For example, if overall diet data are used to describe the predatory relationships of *S. megalops* in southern Australia, the main interactions will be with molluscs, in terms of %W, or with crustaceans, in terms of %N. However, the main interactions will be with teleosts, if sampling is done only in spring, or with molluscs, if only large sharks are collected in summer and autumn, or with crustaceans, if only small sharks are collected in summer and autumn. The same pattern of variability is reported for

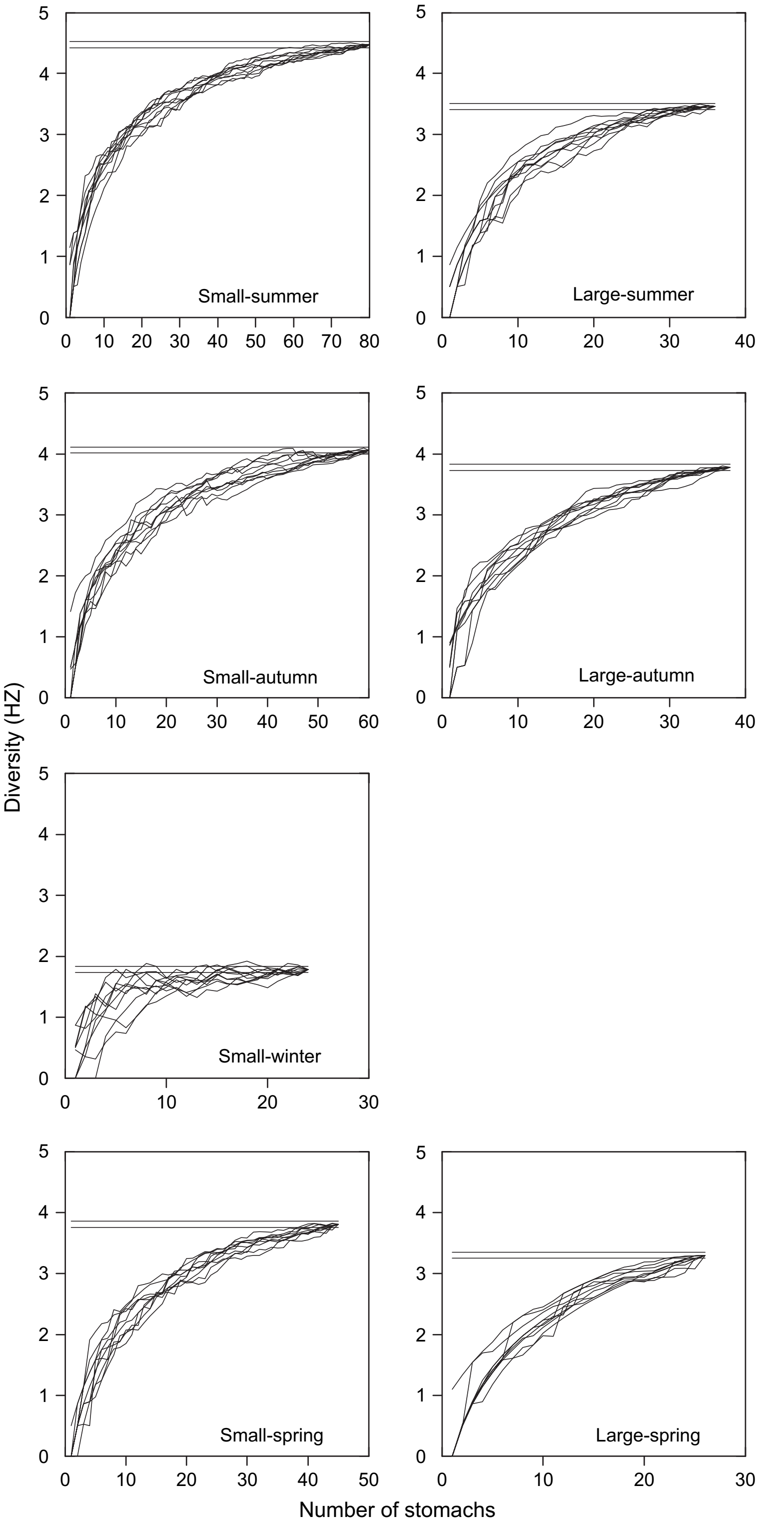

Figure 5. Cumulative diversity (HZ) of prey items for small and large sharks from each season. The straight lines indicate the range of asymptotic diversity ±0.05.

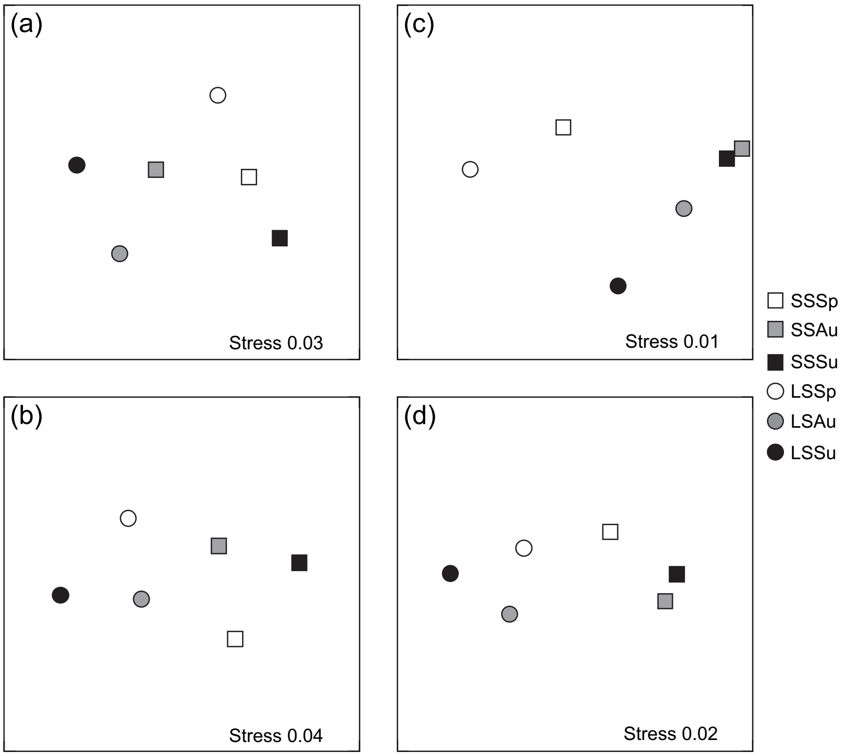

Figure 6. Non-parametric multidimensional scaling (nMDS) ordination of the stomach contents of small sharks from spring (SSSp), autumn (SSAu), and summer (SSSu), and of large sharks from spring (LSSp), autumn (LSAu), and summer (LSSu). Mean %W of (a) ecological and (b) zoological group, and mean %N of (c) ecological and (d) zoological group.

other shark species. Simpfendorfer *et al.* (2001b) compared the diet of tiger sharks from four sites off Western Australia. Overall, the main predatory interactions by %FO were with turtles, teleosts, and sea snakes. However, for one site, North West Shelf, the interactions with teleosts and sea snakes were not as important as with dugongs, and for another site, Ningaloo, tiger sharks interact almost exclusively with turtles. The observed variability in the diet of sharks is particularly relevant when using overall diet data as a descriptor of predator–prey interactions, because the use of overall data may obscure site-, size-, or sex-specific interactions. Also, given that ecosystem-based models tend to use %W data from overall diet as inputs, the occurrence of a few heavy prey items, for example, may overestimate the importance of the interaction between the predator and those particular prey, and underestimate the importance of interactions with other prey.

Size-dependent predation can regulate population and community level dynamics (Brooks and Dodson, 1965), but size-selective feeding has been little studied in sharks. In the present study, *S. megalops* preyed on a wide range of prey size (4–60% of its TL) and, except for cephalopod items, the total length of *S. megalops* was not correlated with size of prey. Other studies found that shark diets consisted of relatively small prey (in most cases, <36% of the sharks TL), and that prey size was correlated to predator size (Cortés *et al.*, 1996; Scharf *et al.*, 2000; Bethea *et al.*, 2004). However, the present study showed that *S. megalops* had little size preference for prey, supporting the belief that this shark is a generalist and opportunistic predator.

Predation can be highly variable in space and time (Bax, 1998). There was regional, seasonal, and ontogenetic variation in the diet of *S. megalops*, and this pattern was consistent despite analyses being conducted on weight or number of zoological or ecological prey groups. Variation was not explained by the effects of sex or maturity condition, but this could be due to the low number of replicates for each combination of factors (e.g. n = 6 for the sex × size × season analysis), and hence low statistical power (Ferry and Cailliet, 1996). Some authors have found differences in the diet of sharks between sexes (Hanchet, 1991; Stillwell and Kohler, 1993; Simpfendorfer *et al.*, 2001b; Koen Alonso *et al.*, 2002) and maturity condition (Koen Alonso *et al.*, 2002). However, some of these studies may have confounded the effects of sex or maturity condition with other factors such as space and time because, although samples were obtained opportunistically across a wide spatial and temporal scale, space and time were not considered in the analyses.

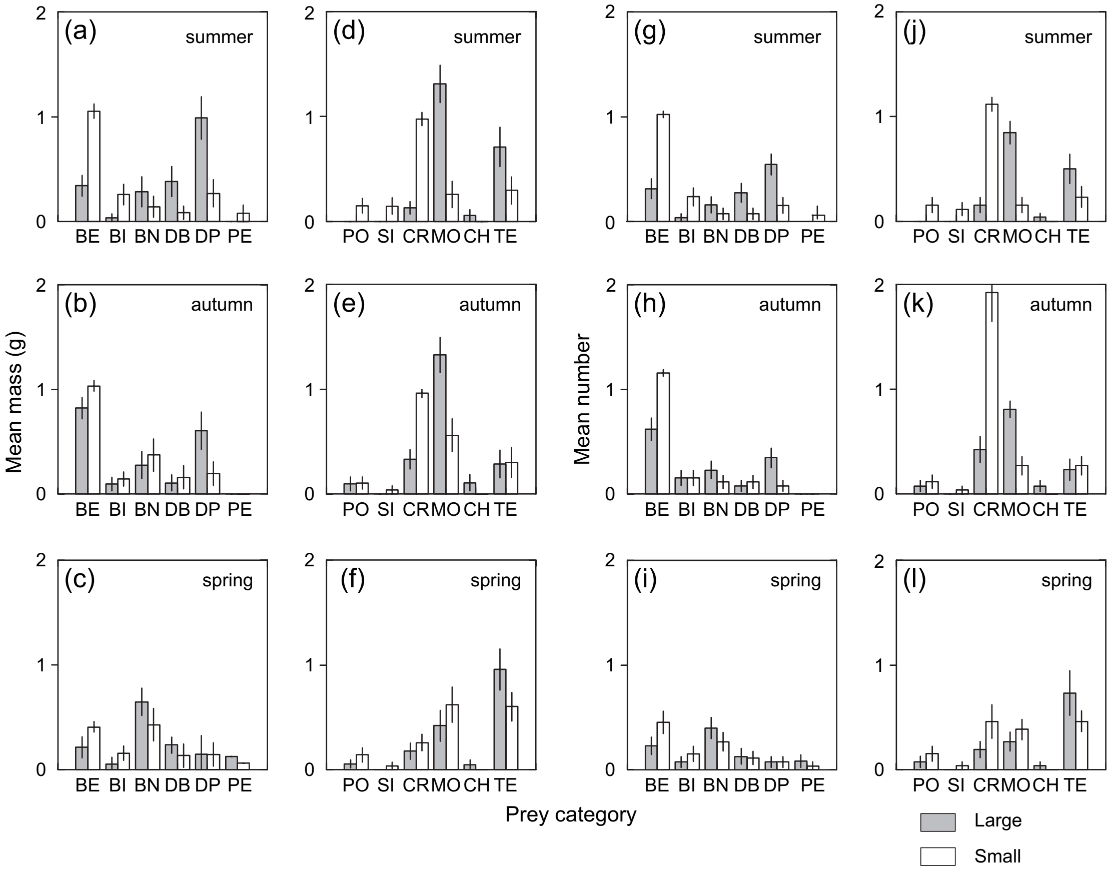

Figure 7. Size and seasonal effects in the diet of large and small *S. megalops* caught in summer, autumn, and spring. The mean weight of fourth root transformed data (±s.e.) of prey sorted by ecological (a, b, c) and zoological group (d, e, f), and the mean number of fourth root transformed data (±s.e.) of prey sorted by ecological (g, h, i) and zoological group (j, k, l). BE, benthic epifauna; BI, benthic infauna; BN, benthic; DB, demersal benthic; DP, demersal pelagic; PE, pelagic. PO, polychaetes; SI, sipunculids; CR, crustaceans; MO, molluscs; CH, chondrichthyans; TE, teleosts.

Feeding plasticity of sharks results in regional, seasonal, and ontogenetic variation in diet that complicates an accurate description of feeding ecology (Wetherbee and Cortés, 2004). However, most studies on the feeding ecology of sharks have described only overall dietary composition. Some studies have reported regional, seasonal, or ontogenetic variation (Jones and Geen, 1977; Lyle, 1983; Laptikhovsky *et al.*, 2001; Simpfendorfer *et al.*, 2001a; Ebert, 2002), but most have done so qualitatively (Wetherbee and Cortés, 2004). When a quantitative approach was taken

Table 5. NP-MANOVA testing for the effects of season (summer, autumn, winter, spring) on the weight and number of zoological (Polychaeta, Sipuncula, Crustacea, Mollusca, Chondrichthyes, Teleosts) and ecological groups (benthic infauna, benthic epifauna, benthic, demersal benthic, demersal pelagic, and pelagic) in the diet of small (<471 mm TL) *S. megalops*.

		Zoological group				Ecological group			
		Weight		Number		Weight		Number	
Factor	d.f.	F	p	F	p	F	p	F	p
Season	3	6.274	<0.001	7.366	<0.001	4.314	<0.001	5.483	<0.001
Residual	92								

(Cortés *et al.*, 1996; Simpfendorfer *et al.*, 2001b; Vögler *et al.*, 2003; White *et al.*, 2004), region, season, or ontogeny were evaluated independently of each other even though samples were collected across wide spatial and temporal scales. When sampling is opportunistic across wide spatial and temporal scales, if the interactive effects of space and/or time are not considered, it is likely that differences in diet attributed to a certain factor (e.g. size) are unknowingly confounded by the effects of other factors (e.g. region) not included in the analysis. Furthermore, if a factor is analysed independently but many factors are involved, the analysis should, at least, be undertaken on standardized data to remove the effects of the other factors not considered.

Standardized data for the effects of season, sex, and size showed regional variation in the diet of large females collected in autumn. Sharks from WWP fed largely on demersal pelagic prey (mainly ommastrephid squid), but those from EWP and NSW had a more varied diet, also consuming benthic prey (teleosts and crustaceans). A demersal pelagic diet implies that a demersal shark such as *S. megalops* undergoes vertical feeding migrations to exploit pelagic prey such as squid or preys on squid while aggregated near the seabed (Roper and Young, 1975). These findings suggest that *S. megalops* would have different patterns of habitat utilization in different areas, interacting in different ecological communities and acting as an energy linkage between them. Although squid occur across the three regions (Norman and Reid, 2000), information on their abundance at a lower scale (regional level) is scarce. Several other shark species show regional variation in dietary composition, switching between prey types with changes in prey availability (Medved *et al.*, 1985; Cortés and Gruber, 1990; Stillwell and Kohler, 1993; Simpfendorfer *et al.*, 2001b). Therefore, it is unclear whether the regional differences found in the diet of *S. megalops* reflect different patterns in feeding and habitat utilization or rather the natural pattern of prey availability. In any case, the present findings reinforce the importance of considering spatial variation as a common phenomenon affecting the feeding ecology of sharks.

Large and small *S. megalops* exploited different resources during part of the year. In summer and autumn, large sharks preyed mostly on demersal pelagic prey (mainly ommastrephid squid), whereas small sharks consumed mainly benthic crustaceans. These ontogenetic differences may be attributed to morphological limitations of small sharks (e.g. gape-limited), better foraging ability of large fish, or differences in the habitat occupied by the two size classes. In spring, however, both size classes had a more varied diet, consuming mainly benthic organisms. Demersal pelagic prey such as squid occur throughout the year, but they show large, unpredictable fluctuations in abundance (Anderson and Rodhouse, 2001). Therefore, the decline in squid consumption shown by large *S. megalops* during spring may be due to a decline in the availability of squid. Collection of data on the seasonal variation in the abundance of squid in the studied area is needed for a better understanding of the seasonal pattern exhibited by large *S. megalops*. Seasonal and ontogenetic variation in diet is common, and it has been reported for a related species, the spiny dogfish (*Squalus acanthias*; Jones and Geen, 1977; Hanchet, 1991; Koen Alonso *et al.*, 2002), and for many other shark species (e.g. Cortés and Gruber, 1990; Simpfendorfer *et al.*, 2001b; White *et al.*, 2004). Cortés *et al.* (1996) found an interaction between season and size of shark in the diet of the bonnethead shark. However, no other study on the diet of sharks has analysed the interaction of these factors when samples from different seasons and size classes were compared. In the present study, an interaction between size and season was found; large and small *S. megalops* had different diets in summer and autumn, but consumed similar prey items in spring. Therefore, the differences found in the dietary composition of large and small *S. megalops* suggest that large and small dogfish would exhibit, at least during part of the year, different predator–prey interactions and ecological roles within the marine ecosystem. Hence, if only the overall diet data are used in an ecosystem model as a proxy for the predator–prey interactions of *S. megalops*, some of the interactions exhibited by this species throughout its lifespan would be ignored.

In conclusion, high variability was found when the overall importance of prey items was estimated. Furthermore, the dietary composition of *S. megalops* varied in space and time, exhibiting differences among regions, seasons, and size classes. Therefore, the intrinsic natural variability in the dietary composition of *S. megalops*, and the spatial and temporal variation in diet exhibited by this opportunistic predator, suggest that studies that infer predator–prey interactions from overall diet are likely to miss information on the ecological relationships among species and therefore account for only part of these interactions. Understanding predator–prey interactions is required for long-term strategic ecosystem management (Bax, 1998). Hence, given that natural variability is intrinsic to ecological systems, the natural variability of predation should be considered when predatory interactions are used to model ecosystem dynamics.

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Appendix

Overall dietary compositions. Prey item sorted by (upper panel) taxonomic, and (lower panel) ecological group. Mean percentage weight (%W), mean percentage number (%N), mean percentage frequency of occurrence (%FO), and mean percentage Index of Relative Importance (%IRI), and 95% confidence intervals. Unid.: unidentifiable; n = 492.

	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Polychaeta	0.62	0.24	1.04	3.26	1.72	4.39	4.32	3.05	5.65	0.27	0.15	0.40
Unid. Polychaeta	0.15	0.04	0.30	1.25	0.60	2.06	1.49	0.72	2.47	0.28	0.09	0.56
Lumbrineridae	0.05	0.01	0.09	0.75	0.25	1.36	0.88	0.29	1.60	0.10	0.02	0.22
Lumbrineris sp.	0.00	0.00	0.01	0.13	0.00	0.39	0.15	0.00	0.46	0.00	0.00	0.01
Nereididae	0.06	0.00	0.16	0.38	0.00	0.86	0.43	0.00	0.91	0.03	0.00	0.08
Eunicidae	0.04	0.00	0.11	0.24	0.00	0.64	0.30	0.00	0.75	0.01	0.00	0.05
Aphroditidae	0.40	0.07	0.89	0.63	0.12	1.21	0.74	0.15	1.47	0.10	0.02	0.25
Sipuncula	0.67	0.22	1.10	1.79	0.90	2.63	1.98	1.11	2.91	0.08	0.03	0.15
Unid. Sipuncula	0.58	0.12	1.22	1.38	0.63	2.17	1.60	0.77	2.55	0.42	0.16	0.82
Sipunculus robustus	0.11	0.00	0.32	0.24	0.00	0.63	0.28	0.00	0.73	0.01	0.00	0.05
Echiura	0.02	0.00	0.07	0.13	0.00	0.39	0.15	0.00	0.57	0.00	0.00	0.02
Crustacea	2.33	1.70	3.22	31.61	28.15	34.86	22.11	19.15	24.79	11.99	9.70	14.22
Unid. Crustacea	0.06	0.00	0.14	0.99	0.13	2.32	0.73	0.15	1.46	0.10	0.01	0.30
Decapoda	0.04	0.01	0.08	0.99	0.36	1.77	1.19	0.45	2.08	0.16	0.05	0.37
Caridea	0.36	0.09	0.74	6.88	2.49	12.22	1.62	0.74	2.56	1.57	0.44	3.18
Palaemonidae	0.00	0.00	0.01	0.26	0.00	0.66	0.30	0.00	0.75	0.01	0.00	0.04
Alpheidae	0.01	0.00	0.04	0.12	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.02
Brachyura	0.02	0.00	0.04	0.38	0.00	0.87	0.44	0.00	1.02	0.02	0.00	0.08
Leucosiidae	0.01	0.00	0.02	0.12	0.00	0.38	0.15	0.00	0.46	0.00	0.00	0.01
Ebalia intermedia	0.01	0.00	0.02	0.12	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.01
Portunidae	0.01	0.00	0.04	0.25	0.00	0.76	0.15	0.00	0.45	0.01	0.00	0.03
Pilumnus sp.	0.02	0.00	0.07	0.25	0.00	0.78	0.15	0.00	0.46	0.01	0.00	0.03
Dendrobranchiata	0.10	0.00	0.27	0.26	0.00	0.65	0.31	0.00	0.75	0.01	0.00	0.05
Solenoceridae	0.01	0.00	0.01	0.38	0.00	0.86	0.45	0.00	1.01	0.02	0.00	0.08
Haliporoides sibogae	0.00	0.00	0.00	0.13	0.00	0.38	0.15	0.00	0.45	0.00	0.00	0.02
Penaeidae	0.14	0.02	0.32	1.85	0.62	3.84	1.31	0.57	2.23	0.35	0.09	0.83
Penaeus sp.	0.02	0.00	0.06	0.26	0.00	0.63	0.30	0.00	0.75	0.01	0.00	0.04
Palinuridae	0.03	0.00	0.11	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.02
Anomura	0.00	0.00	0.01	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.01
Diogenidae	0.34	0.16	0.56	5.90	3.62	8.25	3.79	2.41	5.18	3.15	1.70	4.90
Dardanus arrosor	0.10	0.02	0.21	0.86	0.27	1.50	1.03	0.42	1.86	0.13	0.03	0.30
Strigopagurus strigimanus	0.59	0.19	1.13	2.48	1.40	3.72	2.64	1.59	3.85	1.08	0.53	1.84
Paguristes sp.	0.21	0.12	0.34	5.30	3.02	7.85	3.53	2.35	4.95	2.60	1.32	4.42

(*continued on next page*)

Appendix (*continued*)

	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Paguristes sulcatus	0.02	0.00	0.05	0.25	0.00	0.63	0.29	0.00	0.74	0.01	0.00	0.04
Pagurus sp.	0.03	0.00	0.06	0.37	0.00	0.86	0.43	0.00	1.03	0.02	0.00	0.08
Distosquilla miles	0.03	0.00	0.08	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.02
Austrosquilla osculans	0.01	0.00	0.02	0.12	0.00	0.38	0.15	0.00	0.57	0.00	0.00	0.02
Isopoda	0.06	0.00	0.14	0.62	0.13	1.26	0.73	0.15	1.46	0.07	0.01	0.17
Cirolanidae	0.04	0.01	0.10	0.87	0.24	1.65	0.88	0.29	1.64	0.11	0.02	0.26
Cirolana sp.	0.04	0.01	0.08	1.00	0.38	1.77	1.17	0.45	2.05	0.16	0.04	0.35
Cirolana capricornica	0.01	0.00	0.02	0.25	0.00	0.63	0.29	0.00	0.73	0.01	0.00	0.04
Mollusca	56.43	50.66	62.47	31.45	28.84	34.44	35.89	33.17	38.35	50.31	44.57	54.64
Cephalaspidea	0.15	0.00	0.41	0.37	0.00	0.89	0.45	0.00	1.01	0.03	0.00	0.10
Philine angasi	0.09	0.02	0.19	0.74	0.23	1.37	0.89	0.29	1.76	0.10	0.02	0.24
Volutidae	0.26	0.10	0.49	1.51	0.75	2.43	1.78	0.87	2.85	0.42	0.17	0.80
Fasciolariidae	0.63	0.22	1.13	2.27	1.06	3.81	1.92	0.90	2.97	0.75	0.29	1.42
Turbinidae	0.02	0.00	0.04	0.36	0.00	0.79	0.43	0.00	0.92	0.02	0.00	0.06
Unid. Cephalopoda	2.74	1.32	4.74	2.87	1.84	4.03	3.40	2.14	4.77	2.54	1.37	4.19
Octopus sp.	12.55	7.73	18.03	6.47	4.70	8.23	7.66	5.78	9.54	19.37	12.67	26.35
Octopus pallidus	5.53	1.94	10.02	1.52	0.74	2.42	1.80	0.88	2.80	1.69	0.61	3.32
Octopus warringa	0.78	0.19	1.55	0.75	0.24	1.37	0.90	0.29	1.66	0.19	0.04	0.43
Octopus berrima	1.44	0.44	2.73	1.25	0.50	2.12	1.48	0.60	2.44	0.53	0.18	1.11
Ommastrephidae	20.03	13.84	26.55	7.54	5.76	9.40	8.76	6.73	11.09	32.05	23.78	41.99
Nototodarus gouldi	9.56	4.92	15.38	2.83	1.81	4.01	3.41	2.13	4.75	5.65	2.67	9.39
Todarodes filippovae	0.90	0.06	2.10	0.51	0.12	1.00	0.59	0.14	1.20	0.11	0.01	0.30
Todaropsis eblanae	0.70	0.00	2.17	0.37	0.00	0.84	0.44	0.00	1.03	0.06	0.00	0.23
Ommastrephes bartramii	1.27	0.16	3.32	0.88	0.36	1.53	1.05	0.31	1.80	0.30	0.06	0.75
Histioteuthis sp.	0.05	0.00	0.15	0.13	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.02
Bivalvia	0.01	0.00	0.05	0.13	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.01
Chondrichthyes	1.64	0.50	3.22	1.54	0.52	2.46	1.67	0.83	2.86	0.08	0.03	0.18
Unid. Chondrichthyes	0.03	0.00	0.10	0.13	0.00	0.49	0.15	0.00	0.46	0.00	0.00	0.02
Squalus sp.	0.05	0.00	0.17	0.13	0.00	0.45	0.14	0.00	0.45	0.00	0.00	0.02
Mustelus antarcticus	0.57	0.00	1.91	0.12	0.00	0.39	0.15	0.00	0.45	0.01	0.00	0.08
Urolophidae	0.48	0.00	1.47	0.25	0.00	0.66	0.29	0.00	0.76	0.03	0.00	0.11
Urolophus sp.	0.03	0.00	0.08	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.02
Narcine tasmaniensis	0.31	0.00	0.80	0.49	0.00	1.17	0.45	0.00	0.91	0.05	0.00	0.14
Rajidae	0.28	0.00	0.75	0.24	0.00	0.65	0.29	0.00	0.75	0.02	0.00	0.07
Osteichthyes	38.32	32.71	43.92	30.34	26.95	33.51	34.03	30.74	36.98	37.27	32.73	42.93
Unid. Osteichthyes	2.58	1.43	4.14	4.61	3.24	6.05	5.45	3.83	7.18	5.23	3.21	7.74
Anguilliformes	0.04	0.00	0.14	0.13	0.00	0.39	0.15	0.00	0.46	0.00	0.00	0.02

Scolecenchelys sp.	0.13	0.00	0.33	0.37	0.00	0.86	0.44	0.00	1.03	0.03	0.00	0.09
Scolecenchelys breviceps	0.05	0.00	0.12	0.36	0.00	0.87	0.44	0.00	1.04	0.02	0.00	0.08
Serrivomer sp.	0.17	0.01	0.41	0.50	0.12	1.04	0.59	0.14	1.20	0.05	0.00	0.14
Congridae	0.24	0.00	0.77	0.12	0.00	0.38	0.15	0.00	0.45	0.01	0.00	0.04
Clupeidae	2.03	0.74	3.68	1.51	0.61	2.58	1.47	0.59	2.53	0.70	0.26	1.41
Paraulopus nigripinnis	0.54	0.00	1.49	0.25	0.00	0.64	0.29	0.00	0.74	0.03	0.00	0.11
Myctophidae	0.46	0.00	1.15	0.36	0.00	0.85	0.44	0.00	1.02	0.05	0.00	0.14
Macrouridae	1.49	0.21	3.09	0.77	0.25	1.43	0.92	0.30	1.64	0.28	0.07	0.63
Caelorinchus sp.	0.24	0.00	0.64	0.24	0.00	0.63	0.28	0.00	0.75	0.02	0.00	0.07
Lepidorhynchus denticulatus	0.54	0.13	1.09	0.85	0.24	1.69	0.87	0.15	1.65	0.16	0.03	0.38
Macruronus novaezelandiae	0.18	0.00	0.62	0.13	0.00	0.49	0.15	0.00	0.45	0.01	0.00	0.03
Cyttidae	1.25	0.00	3.34	0.24	0.00	0.64	0.29	0.00	0.75	0.06	0.00	0.24
Cyttus australis	0.27	0.00	0.89	0.12	0.00	0.38	0.14	0.00	0.45	0.01	0.00	0.04
Macroramphosidae	0.22	0.01	0.65	0.50	0.11	1.08	0.59	0.14	1.29	0.06	0.00	0.16
Macroramphosus scolopax	0.17	0.01	0.42	0.51	0.12	1.02	0.60	0.14	1.21	0.06	0.01	0.15
Centriscops sp.	0.30	0.00	0.98	0.12	0.00	0.39	0.15	0.00	0.46	0.01	0.00	0.04
Triglidae	9.77	6.02	13.83	5.33	3.83	7.07	5.97	4.25	7.71	12.00	7.51	17.14
Lepidotrigla sp.	0.11	0.00	0.37	0.13	0.00	0.39	0.15	0.00	0.45	0.00	0.00	0.02
Lepidotrigla mulhalli	0.34	0.00	0.87	0.36	0.00	0.84	0.43	0.00	1.02	0.04	0.00	0.12
Lepidotrigla modesta	1.37	0.17	3.21	0.75	0.13	1.53	0.74	0.15	1.45	0.21	0.03	0.54
Chelidonichthys kumu	0.27	0.00	0.84	0.13	0.00	0.39	0.15	0.00	0.45	0.01	0.00	0.04
Platycephalidae	0.13	0.00	0.39	0.25	0.00	0.64	0.30	0.00	0.76	0.01	0.00	0.05
Neoplatycephalus conatus	0.37	0.00	0.89	0.38	0.00	0.85	0.45	0.00	1.01	0.05	0.00	0.13
Scorpaenidae	0.22	0.00	0.75	0.13	0.00	0.39	0.15	0.00	0.46	0.01	0.00	0.04
Helicolenus percoides	0.39	0.00	1.24	0.24	0.00	0.78	0.14	0.00	0.45	0.01	0.00	0.06
Perciformes	0.18	0.00	0.61	0.12	0.00	0.40	0.15	0.00	0.47	0.01	0.00	0.03
Acropomatidae	0.88	0.00	2.59	0.25	0.00	0.63	0.29	0.00	0.74	0.04	0.00	0.16
Apogonops anomalus	2.38	1.32	3.71	4.48	2.81	6.40	4.12	2.80	5.61	3.77	2.15	5.88
Gempylidae	1.88	0.53	3.56	1.35	0.58	2.29	1.45	0.60	2.33	0.63	0.22	1.22
Thyrsites atun	0.50	0.00	1.27	0.24	0.00	0.62	0.29	0.00	0.74	0.03	0.00	0.10
Sillago flindersi	0.29	0.00	0.98	0.12	0.00	0.38	0.15	0.00	0.57	0.01	0.00	0.04
Parequula melbournensis	1.43	0.32	2.92	1.12	0.25	2.17	0.90	0.29	1.66	0.31	0.07	0.66
Carangidae	0.28	0.00	0.87	0.23	0.00	0.63	0.29	0.00	0.74	0.02	0.00	0.07
Trachurus sp.	0.40	0.00	1.28	0.13	0.00	0.41	0.15	0.00	0.45	0.01	0.00	0.05
Trachurus declivis	0.87	0.00	2.93	0.13	0.00	0.39	0.15	0.00	0.45	0.02	0.00	0.11
Scomber australasicus	3.50	1.56	6.06	1.62	0.80	2.59	1.93	1.02	3.02	1.32	0.54	2.47
Apogonidae	0.12	0.00	0.37	0.13	0.00	0.40	0.15	0.00	0.46	0.01	0.00	0.02
Argentina elongata	0.06	0.00	0.18	0.25	0.00	0.65	0.30	0.00	0.74	0.01	0.00	0.05
Otariidae	0.79	0.00	2.67	0.12	0.00	0.38	0.14	0.00	0.45	0.02	0.00	0.10
Unid. Porifera	0.00	0.00	0.01	0.12	0.00	0.49	0.15	0.00	0.58	0.00	0.00	0.02
Unid. Hydrozoa	0.00	0.00	0.00	0.12	0.00	0.39	0.14	0.00	0.45	0.00	0.00	0.01

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Appendix (*continued*)

	%W			%N			%FO			%IRI		
Prey	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%	Mean	Lower 95%	Upper 95%
Unid. Algae	0.01	0.00	0.04	0.12	0.00	0.38	0.15	0.00	0.45	0.00	0.00	0.01
Unid. Ophiuroidea	0.00	0.00	0.00	0.12	0.00	0.38	0.15	0.00	0.45	0.00	0.00	0.01

	%W			%N			%FO			%IRI		
Prey	Mean	Upper 95%	Lower 95%	Mean	Upper 95%	Lower 95%	Mean	Upper 95%	Lower 95%	Mean	Upper 95%	Lower 95%
Benthic epifauna	4.02	5.25	2.87	41.15	46.80	35.61	29.41	32.78	26.12	30.70	35.62	25.72
Benthic infauna	1.24	1.99	0.65	5.86	7.71	4.22	7.56	9.69	5.62	1.24	1.78	0.80
Benthic	36.95	43.97	30.18	21.10	24.53	17.70	25.34	28.91	21.90	33.96	40.28	28.08
Demersal benthic	11.04	14.75	7.50	11.10	14.02	8.59	12.24	14.93	9.84	6.27	8.42	4.49
Demersal pelagic	40.25	48.22	32.30	16.41	19.51	13.62	20.25	23.54	17.26	26.52	32.34	21.17
Pelagic	6.49	10.00	3.64	4.38	6.08	2.85	5.19	7.21	3.54	1.31	2.08	0.79

Hierarchical approach to the assessment of fishing effects on non-target chondrichthyans: case study of *Squalus megalops* in southeastern Australia

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Abstract: A three-levelled hierarchical risk assessment approach was trialed using piked spurdog (*Squalus megalops*) to evaluate the suitability of the approach for chondrichthyan species. At level 1, a qualitative assessment indicated that the only fishing-related activity to have moderate or high impact on *S. megalops* was "capture fishing" by otter trawl, Danish seine, gillnet, and automatic longline methods. At level 2, a semi-quantitative assessment ranked *S. megalops* at risk because of its low biological productivity and, possibly, its catch susceptibility from cumulative effects across the separate fishing methods. Finally, at level 3, a quantitative assessment showed that population growth is slow even under the assumption of density-dependent compensation where the fishing mortality rate equals the natural mortality rate. Although published information indicates that relative abundance has been stable in several regions of southern Australia, it is concluded that given its low biological productivity, changed fishing practices leading to increased fishing mortality could quickly put *S. megalops* at high risk. The hierarchical approach appears particularly useful for assessment of chondrichthyan species in data-limited fisheries. This approach allows for a management response at any level, optimizing research and management efforts by identifying and excluding low-risk species from data intensive assessments.

Résumé : Nous employons une méthode hiérarchique à trois niveaux pour l'évaluation des risques chez le requin aiguillat (*Squalus megalops*) afin de vérifier si la méthode s'applique aux espèces de chondrichthyens. Au niveau 1, une évaluation qualitative indique que la seule activité de pêche qui ait un impact modéré ou élevé sur *S. megalops* est la « pêche de capture » faite par les méthodes du chalut à panneaux, de la seine danoise, du filet maillant et de la palangre automatique. Au niveau 2, une évaluation semi-quantitative considère *S. megalops* à risque à cause de sa faible productivité biologique et, peut-être, sa susceptibilité à la capture due aux effets cumulatifs des différentes techniques de pêche. Enfin, au niveau 3, une évaluation quantitative montre que la croissance de la population est lente, même si on assume une compensation dépendante de la densité dans laquelle le taux de mortalité due à la pêche est égal au taux de mortalité naturelle. Bien que les informations publiées indiquent que l'abondance relative de *S. megalops* est stable dans plusieurs régions du sud de l'Australie, nous concluons qu'à cause de sa faible productivité biologique, des changements dans les pratiques de pêche qui mèneraient à une mortalité accrue due à la pêche pourraient placer l'espèce dans une position de grand risque. La méthode hiérarchique semble particulièrement utile pour l'évaluation des espèces de chondrichtyens dans des pêches commerciales pauvres en données. Cette approche permet une réaction de gestion, à divers niveaux, et elle optimise les efforts de recherche et de gestion en identifiant et en excluant les espèces à faible risque des évaluations fondées sur des bases importantes de données.

[Traduit par la Rédaction]

Introduction

Globally, only limited attempts have been made to manage populations of chondrichthyan species impacted by the effects of fishing (Anderson 1990; Bonfil 1994). The few exceptions have focused on target species such as gummy shark (*Mustelus antarcticus*) (Walker 1998), school shark (*Galeorhinus galeus*) (Punt et al. 2000), and dusky shark (*Carcharhinus obscurus*) (Simpfendorfer 1999) in southern Australia. Although biological parameter estimates and time series of catch, fishing effort, and other monitoring data have been collected to enable stock assessment for sustainable use of the high-valued species, there is a paucity of such information for non-target species (Bonfil 2004). Given the comparatively low biological productivity and often high catch susceptibility of chondrichthyan species (Stobutzki et al. 2002; Walker 2004), management initiatives are needed long before sufficient data can be collected for stock assessment

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(Walker 2004). Concerns about widespread depletion of chondrichthyan populations led the United Nations Food and Agricultural Organization (FAO) to develop an International Plan of Action for the Conservation and Management of sharks (IPOA sharks) (FAO 2000) that was implemented during 1999.

More recently, to address the concerns of uncertainty associated with the wider impacts of fishing on marine ecosystems, Australia is developing and implementing a broad process for ecological assessment in a risk framework. This process is referred to as ecological risk assessment and explicitly identifies five ecological components for analysis: target species, non-target species comprising by-product (predominantly retained) and by-catch (predominantly discarded), threatened species, fish habitats, and ecological communities. Within each component, for each type of fishing method separately, the approach involves a three-levelled hierarchical process of assessment, with increasing data requirements and complexity when progressing from level 1, through level 2, to level 3 assessment. Level 1 assessment involves expert judgement and determines whether or not there is a need to progress to level 2 or, alternatively, to implement a management response. Level 2 assessment is semi-quantitative and determines whether or not there is a need to progress to level 3 or, alternatively, to implement a management response. When progressing from one level to the next, depending on costs, there is the choice of either immediately initiating a management response to ameliorate risk of adverse effects or, alternatively, proceeding to invest in research and monitoring to enable a higher level of assessment (Hobday et al. 2006; Smith et al. 2006). This approach to ecological risk assessment would be exhaustive if all components were taken to level 3 and would require excessive costs in a multispecies fishery.

The purpose of the present study is simply to take a single chondrichthyan species — the piked spurdog (*Squalus megalops*) — for which sufficient data are available to undertake an assessment at each of the three levels and to evaluate the suitability of the approach for chondrichthyan species in general. *Squalus megalops* falls within the non-target component and is one of the most abundant and widespread chondrichthyan species impacted by Australia's Southern and Eastern Scalefish and Shark Fishery (SESSF). The species is mostly taken as by-catch by demersal trawl on the continental shelf and upper slope (~600 tonnes (t) per annum) (Walker and Gason 2006). Small quantities are also taken on the upper slope by automatic longline targeted at teleost species and on the continental shelf by gillnets deployed in the targeted shark fishery for *M. antarcticus* (Walker and Gason 2005; Walker et al. 2005). Because of long-term declines in abundance of shark and chimaera populations off New South Wales, southeastern coast of Australia (Graham et al. 2001), quota reductions on target and by-product shark and chimaera species, and growing consumer demand for shark meat, some large individuals of *S. megalops* are beginning to be retained for marketing (Walker and Gason 2005).

Materials and methods

Squalus megalops was assessed using the Australian process for ecological risk assessment as part of the non-target component at each of the three hierarchical levels. Progressing through the three levels, level 1 involved qualitative assessment based on expert judgement, level 2 involved semi-quantitative assessment, and level 3 involved fully quantitative assessment based on available data. The approaches to level 1 and level 2 assessments are explicitly prescribed (Hobday et al. 2006), and Australia has extensive experience with stock assessment of target and by-product species in a risk framework (level 3 assessment). However, the process is not presently explicit for level 3 assessment of non-target species where catches are not known precisely. The present study applies an approach that assumes no knowledge of catches and catch rates.

Table 1. Description of the potential impacts of different fishing activities on *S. megalops*.

Impact	Fishing activity
Direct	Capture (damage or mortality due to gear deployment, including discards)
	Cryptic mortality (unaccounted damage or mortality due to interactions with fishing gear)
	Gear loss (damage or mortality without capture due to interactions with gear lost from the fishing vessel)
Indirect	Species translocation (introduction of species to the habitat of the assessed species)
	On-board processing and catch discarding (discard of unwanted parts of target species or unwanted organisms from the catch)
	Provisioning (use of bait or burley)
	Pollution (introduction of chemical and physical pollutants from fishing vessels, such as exhaust, oil spills, detergents, rubbish, lost gear, noise)

Note: Direct impacts are impacts causing damage or mortality, whereas indirect impacts are impacts altering the habitat of the species (adapted from Hobday et al. 2006).

Level 1 assessment

Level 1 assessment was a qualitative analysis for each fishing method that may impact *S. megalops* based on expert knowledge (J.M.B. and T.I.W.). Adopting the precautionary approach, the species was assigned the highest risk value if there was uncertainty about risk judgement (Hobday et al. 2006). The fishing methods in the SESSF that may have an effect on *S. megalops* in southern Australia are otter trawl and Danish seine nets, demersal shark gillnets, demersal shark longlines, automatic longlines, droplines, and traps and pots. Within these fishing methods, seven associated activities (explained in Table 1) may impact *S. megalops*. Each fishing-related activity within the non-target component was assessed using spatial- and temporal-scale, intensity, and consequence analyses (Hobday et al. 2006). This approach involved assigning a score to each of spatial and temporal scale, intensity, and consequence of the fishing activity (explained in Table 2). Fishing methods with fishing activities with a consequence score ≤2 were eliminated from further assessments, whereas methods with higher scores underwent more in-depth assessment at level 2.

Level 2 assessment

For level 2, the species was assessed based on its biological

Table 2. Description of the score values for the spatial and temporal scale and intensity and consequence of the fishing activities (adapted from Hobday et al. 2006).

Score	Spatial scale (nm)	Temporal scale	Intensity	Consequence
1	<1	Decadal	Negligible (remote likelihood of detection)	Negligible (impact unlikely to be measured)
2	1–10	Every several years	Minor (seldom occurring and rare to detect)	Minor (minimal impact on stock size, structure, or dynamics)
3	10–100	Annual	Moderate (moderate at broader scale, or severe but local)	Moderate (medium impact on stock size, structure, or dynamics)
4	100–500	Quarterly	Severe (severe and occurring often at broad scale)	Major (wider and longer term impact on stock size, structure, or dynamics)
5	500–1000	Weekly	Major (occasional but very severe and localized or frequent and widespread but less severe)	Extreme (serious impact on stock size, structure, or dynamics with long time period to restore to acceptable levels)
6	>1000	Daily	Catastrophic (local to regional severity or continual and widespread)	Intolerable (widespread and irreversible impact on stock size, structure, or dynamics)

productivity and catch susceptibility. Biological productivity can be inferred from the reproductive rate or the natural mortality rate of a species assuming that with immigration and emigration being equal, there has to be a balance between reproductive rate and natural mortality rate for a population to remain in equilibrium (Walker 2004). Species with low reproductive rate and low natural mortality have low biological productivity and, hence, are at higher risk from the effects of fishing than species with high biological productivity. For *S. megalops*, natural mortality (*M*) was used as a proxy for biological productivity. Natural mortality was estimated by five indirect life-history methods described elsewhere (e.g., Cortés 2002), and the mean value was used. The indirect methods of Pauly (1980), Hoenig (1983), and Chen and Watanabe (1989) and two methods by Jensen (1996) use parameters estimated from the von Bertalanffy growth model (VBGM) and maximum age information obtained from Braccini (2006) for *S. megalops*. Pauly's (1980) method also uses information on the mean value of water temperature (14.6 °C) that was taken from http://www.marine.csiro.au. Based on empirical data, Walker (2004) devised a scale for M categorization where values of $M \leq 0.16$, between 0.16 and 0.38, and ≥ 0.39 correspond to low, moderate, and high biological productivity, respectively. This scale was used for biological productivity categorization of *S. megalops*.

Catch susceptibility, a measure of the extent of the fishing impact of each fishing method, is the product of availability (proportion of the spatial distribution of the population that is fished by the fishing method, based on the assumption of an even distribution of fishing method and species), encounterability (proportion of the available population encountered by one unit of fishing effort), selectivity (proportion of the encountered population that is captured by the fishing gear), and post-capture mortality (proportion of captured animals that die) (Walker 2004). Each of these fishing parameters ranges from 0 to 1; hence, catch susceptibility also ranges from 0 to 1. Fishing parameters with assigned values of 0.33, 0.66, and 1.00 (upper value for each one-third range) are designated low, moderate, and high, respectively (Table 3; Walker 2004). Based on expert judgement and the precautionary approach (i.e., high if unknown), the availability, encounterability, selectivity, post-capture mortality, and catch susceptibility of *S. megalops* were determined for each fishing method.

A species identified as having low biological productivity with moderate to high catch susceptibility would be considered to be at high risk and need to be assessed at level 3. A species with moderate to high biological productivity and low catch susceptibility would be considered to be at low risk and require no further assessment.

Level 3 assessment

Level 3 assessment involved a quantitative data-intensive analysis. Application of biomass dynamic models or more complex models requires time series of catch, fishing effort, and relative abundance data, which are not available for most shark species, particularly by-catch species. Given that demographic analyses require only life-history parameters, which are commonly available for many species, this approach was used to make the assessment more compatible and applicable to a broader suite of fisheries. The assessment involved the quantitative estimation of population growth rate, elasticities, rebound potential, and population doubling time.

Population growth rate ($\lambda = e^r$, where r is the population instantaneous rate of increase) and elasticities (effect of a proportional change in a vital rate on population growth rate) were estimated using a birth-flow Leslie matrix (Caswell 2001). Elasticities of fertility, juvenile survival, and adult survival are normally obtained by summation of matrix element elasticities across relevant age classes (e.g., Caswell 2001; Carlson et al. 2003). However, in the present study, age-at-maturity of *S. megalops* was not assumed to be knife-edged, rather it was determined from an ogive produced by

Table 3. Description of the score values of fishing parameters for three arbitrary risk categories (adapted from Walker 2004).

	Risk category		
Parameter	Low	Moderate	High
Availability	0.33 (fishery ranges < one-third of species range)	0.66 (fishery ranges one-third to two-thirds of species range)	1.00 (fishery ranges > two-thirds of species range)
Encounterability	0.33 (0–0.33 probability of species encountering the gear, e.g., pelagic species encountering bottom trawl net)	0.66 (0.33–0.66 probability of species encountering the gear, e.g., pelagic species encountering mid-water trawl net)	1.00 (0.67–1.00 probability of species encountering the gear, e.g., bottom-dwelling species encountering bottom trawl net)
Selectivity	0.33 (0–0.33 probability of species being caught by the gear, e.g., filter-feeder species taking a baited hook)	0.66 (0.33–0.66 probability of species being caught by the gear, e.g., fast-swimming species taken by bottom trawl net)	1.00 (0.67–1.00 probability of species being caught by the gear, e.g., species with protruding structures taken by gillnet)
Post-capture mortality	0.33 (0.67–1.00 probability of survival after capture, e.g., discarded bottom-dwelling species with spiracles and robust structure)	0.66 (0.33–0.66 probability of survival after capture, e.g., discarded species with a fragile structure and ram-jet ventilation)	1.00 (0–0.33 probability of survival after capture, e.g., retained target and by-product species)
Catch susceptibility	0–0.33	0.33–0.66	0.67–1.00

Note: Catch susceptibility is the product of availability, encounterability, selectivity, and post-capture mortality.

Braccini et al. (2006). Hence, for each age class, the survival elasticity of juveniles and adults was the product of the elasticity and the proportion of juvenile and adult females within each class. The total juvenile and adult elasticity was then obtained by summing across the different age classes. Population rebound potential (r_z, where z is total mortality) and doubling time ($T_D = \ln(2)\cdot r_z^{-1}$) were estimated by the method of Smith et al. (1998), which incorporates density-dependent compensation of adult M through preadult survival. Rebound potential is calculated at the population level of maximum sustainable yield (Smith et al. 1998).

To explore sensitivity to error and (or) variation in life-history parameter estimates, a probability density function (pdf) was developed for each life-history parameter following the approach of Cortés (2002) and Carlson et al. (2003). The pdfs were then used in a Monte Carlo simulation (with 10 000 iterations) to incorporate uncertainty in the estimation of population parameters. Each iteration involved the random selection of a set of life-history parameter values and the calculation of λ, elasticities, r_z, and T_D. In this way, prediction intervals (2.5th and 97.5th percentiles) were obtained from the probability density distribution for each of the estimated population parameters. Simulations were run using Microsoft Excel spreadsheets equipped with the add-in PopTools version 2.6 (http://www.cse.csiro.au/poptools/) and a risk assessment software (Crystal Ball; Decisioneering Inc., Denver, Colorado) lent by E. Cortés (NOAA, Southeast Fisheries Science Centre, Panama City, Florida).

Life-history parameters needed for the estimation of population parameters were obtained from the literature. Average litter size, the relationship between fecundity and total length (TL) of female, embryo sex ratio, length-at-maturity, and length-at-maternity (relationship between the proportion of females in maternal condition, i.e., contributing to annual recruitment, and TL) were obtained from Braccini et al. (2006). Average litter size was assumed to follow a normal pdf with a mean (and standard deviation, SD) of 2.32 (0.48) and a lower and upper bounds of 2 and 4, respectively, reflecting the range of litter sizes reported. The fecundity–TL relationship was predicted from the linear equation, litter size = 0.0071(0.001)TL – 1.503(0.549), and the error structure around estimates of fecundity parameters was represented by a normal pdf. The embryo sex ratio reported for *S. megalops* was 1:1 so a 0.5 factor was used to half the litter size–TL function and obtain the number of female embryos per female. Length-at-maternity was predicted from the following logistic equation:

$$\text{proportion maternal} = 0.5(1 + e^{-\ln(19)((\mathrm{TL}-31(18))/(626(47)-531(18)))})^{-1}$$

and the error structure around estimates of maternity parameters was represented by a normal pdf. Growth parameters and maximum age were obtained from Braccini (2006). The growth equation for females was used to transform the relationships between the reproductive variables and TL to relationships between reproductive variables and age. Natality-at-age was calculated as the product of 0.5 (embryo sex ratio), the age-at-fecundity, and the age-at-maternity functions. Two extreme case scenarios were considered. The first is deemed as the worst-case scenario, whereas the second scenario is the more optimistic.

In the first scenario, growth parameters (and standard error, SE) L_∞ = 756 (45) mm, k = 0.042 (0.005) year^{-1}, and t_0 = –9.77 (1.30) years produced by a two-phase VBGM were used as the most likely values in a normal pdf. The error structure around estimates of age at 50% maturity was represented by a triangular pdf with 15 as the most likely value and ±2 years as the lower and upper bounds. These values were derived from a length-at-maturity curve (Braccini et al. 2006) and the growth curve produced by the two-phase VBGM. The error structure around estimates of maximum age was represented by a linearly decreasing pdf scaled to 1, with the most likely value of 28 (oldest shark aged by Braccini 2006) and the lower bound set by arbitrarily adding 30% to the most likely value, i.e., 36 (Cortés 2002). Annual survivorship-at-age for the Leslie matrix was assumed to be uniform, ranging from 0.862 to 0.936, estimated by the Hoenig (1983) and Jensen (1996) methods, respectively. Adult M for the Smith et al. (1998) method was also assumed to have a uniform pdf ranging from 0.066 to 0.149. Maximum sustainable yield for the Smith et al. (1998) method was assumed to occur at total mortality (Z) = 1. 5M.

In the second scenario, growth parameters $L_\infty = 699$ (17) mm and $k = 0.056$ (0.005) year^{-1} produced by a two-parameter VBGM growth model were used as the most likely values in a normal pdf. The error structure around estimates of age at 50% maturity was represented by a triangular pdf with 14 as the most likely value and ±2 years as the lower and upper bounds. These values were derived from the length-at-maturity curve and the growth curve produced by the two-parameter VBGM growth. Maximum age was represented as in the first scenario, with the difference that the maximum bound was set to 50% of the most likely value, i.e., 42. Annual survivorship-at-age for the Leslie matrix was assumed to be uniform, ranging from 0.930 to 0.936, estimated by the Chen and Watanabe (1989) and Jensen (1996) methods, respectively. Adult M for the Smith et al. (1998) method was also assumed to have a uniform pdf ranging from 0.066 to 0.072. Maximum sustainable yield for the Smith et al. (1998) method was assumed to occur at Z = 2M.

A Spearman rank correlation (r_S) was used to measure possible correlation between life-history parameters and λ. For each scenario, the correlation between the simulated M, k, the slope of the fecundity curve, and TL at 50% maturity of the length-at-maternity relationship with the forecasted λ was determined. A modified Bonferroni method was used to correct for multiple hypothesis testing (Jaccard and Wan 1996). Individual comparisons were rank-ordered from most to least significant and a significance cutoff for the most significant correlation was determined by dividing the significance level of 0.05 by 8, the number of comparisons made. If the most significant correlation was found to be significant, a new significance cutoff for the second most significant correlation was determined by dividing the significance level of 0.05 by 7. This stepwise backwards elimination procedure was used for determining the significance cutoff for the remainder of the correlations.

Results

Level 1 assessment

Level 1 assessment of the fishing methods indicated that the only fishing-related activity to have moderate or higher consequences on the sustainability of *S. megalops* was that associated with "capture fishing" (Appendix A, Table A1). Other activities had either negligible or minor consequences. Among methods, capture fishing of shark longlines, droplines, and traps and pots had a negligible effect on *S. megalops* because of their recent decline to ~0 effort in 2004 (Walker and Gason 2006). Hence, these methods were not assessed at a second level. Conversely, capture fishing for the otter trawl, Danish seine, shark gillnet, and automatic longline methods had a consequence score >2, so these fishing methods need to be assessed at level 2.

Level 2 assessment

Estimates of natural mortality (M) had a mean value of 0.085, ranging from 0.066, for one of Jensen (1996) methods, to 0.149 (Hoenig 1983), indicating that *S. megalops* had low biological productivity (i.e., $M \leq 0.16$). Catch susceptibility of *S. megalops* varied depending on the fishing method (Appendix A, Table A2). For the shark gillnet method, given the low selectivity and moderate availability and post-capture mortality, catch susceptibility was low (catch susceptibility = 0.66 × 1.00 × 0.33 × 0.66 = 0.14). For the automatic longline method, catch susceptibility was also low, as availability was low (catch susceptibility = 0.33 × 1.00 × 1.00 × 0.66 = 0.22). For the otter trawl and Danish seine methods, there is uncertainty regarding the extent of their spatial overlap with *S. megalops* distribution. If availability for these fishing methods was designated low, catch susceptibility was also low (catch susceptibility = 0.33 × 1.00 × 1.00 × 1.00 = 0.33). However, if availability was considered moderate, catch susceptibility was also moderate because of high encounterability, selectivity, and post-capture mortality (catch susceptibility = 0.66 × 1.00 × 1.00 × 1.00 = 0.66). In addition, cumulative effects across the four fishing methods may cause an underestimation of total catch susceptibility; hence, based on *S. megalops* low biological productivity, this species was classed as at high risk and needed to be assessed at level 3.

Level 3 assessment

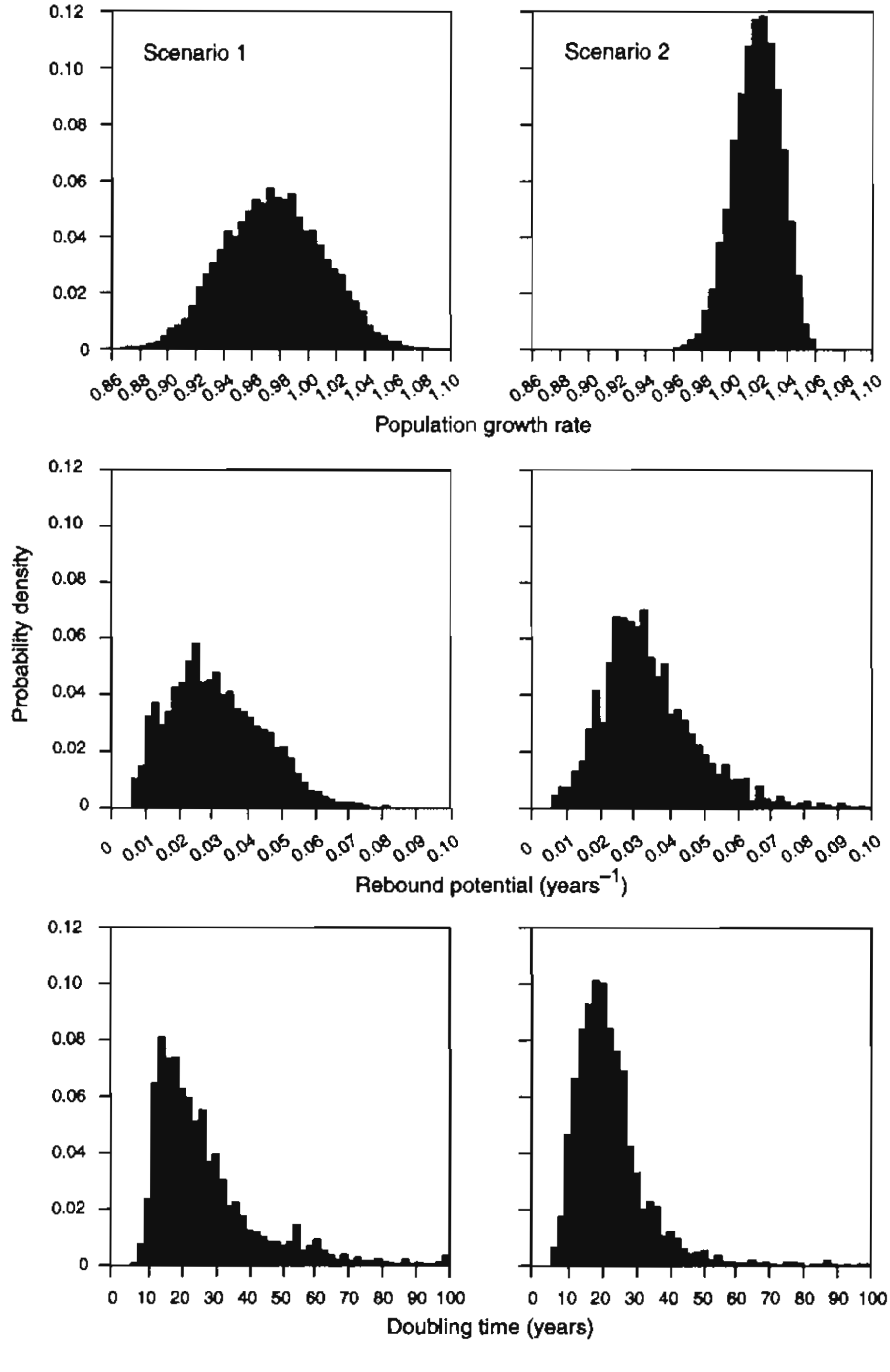
For the first (worst-case) scenario, population growth rate (λ) averaged 0.975 (median 0.974, 95% confidence interval (CI) 0.974–0.976) (Fig. 1). Fertility elasticities averaged 0.046 (0.045, 0.046–0.046), elasticities of juvenile survival were 0.630 (0.629, 0.628–0.631) and those of adults were 0.325 (0.325, 0.323–0.326). Rebound potential (r_z) averaged 0.031 year^{-1} (0.029, 0.030–0.032) and population doubling time (T_D) was 28.2 years (23.5, 27.9–28.5) (Fig. 1). There was a negative correlation between M and λ ($r_S = -0.685$, $P = 0.006$) and between TL$_{50}$ (TL at 50% maturity) and λ ($r_S = -0.139$, $P = 0.025$). There was a positive correlation between the growth coefficient (k) and λ ($r_S = 0.474$, $P = 0.008$) and between the fecundity slope and λ ($r_S = 0.284$, $P = 0.017$).

For the second (more optimistic) scenario, λ averaged 1.018 (median 1.019, 95% CI 1.017–1.019) (Fig. 1). Fertility elasticities averaged 0.045 (0.045, 0.045–0.045), elasticities of juvenile survival were 0.397 (0.395, 0.396–0.398) and those of adults were 0.559 (0.560, 0.558–0.560). Rebound potential averaged 0.035 year^{-1} (0.032, 0.035–0.035) and T_D was 23.7 years (21.4, 23.5–23.9) (Fig. 1). There was a negative correlation between M and λ ($r_S = -0.111$, $P = 0.050$) and between TL$_{50}$ and λ ($r_S = -0.314$, $P = 0.013$). There was a positive correlation between k and λ ($r_S = 0.342$, $P = 0.010$) and between the fecundity slope and λ ($r_S = 0.638$, $P = 0.007$).

Discussion

Conservation and management of marine resources should be based on the integration of qualitative and quantitative methods (Cortés 2004) simply because management based solely on quantitative information is of limited application to data-poor fisheries (Johannes 1998). Qualitative, semi-quantitative, and quantitative data together in a hierarchical assessment framework showed that *S. megalops* is potentially

Fig. 1. Probability density distribution of population growth rate, rebound potential, and population doubling time for scenarios 1 and 2 (N = 10 000 simulations).



highly susceptible to the effects of fishing. At a qualitative level (level 1), the hierarchical assessment allowed screening out of fishing methods and fishing-related activities considered to pose low risk to this species. This indicates that research effort should be allocated to those fishing methods and fishing activities (capture fishing) leading to moderate or higher impacts on *S. megalops*. At this level, expert opinion should include a range of stakeholders who understand the interactions between fishing methods and the biology of the species (scientists, managers, fishers). Qualitative expert judgement, e.g., knowledge possessed by artisanal fishers, has been valuable for successful management of tropical fisheries in developing countries (Johannes 1998). Furthermore, expert knowledge is commonly used in Bayesian (e.g., Martin et al. 2005) and fuzzy logic (Cheung et al. 2005) modelling for conservation assessments. Hence, quantitative information need not be an exclusive condition for sound management; a qualitative assessment of chondrichthyans would allow ruling out of species ranked at low risk, allowing focus on those at high risk. The value of this approach is twofold. First, it is usually not practical to undertake long-term studies on non-target chondrichthyan species because of an urgent need for their effective management. Second, the Australian ecological risk assessment process is valuable at making research more cost-effective and at prioritising research funding involving high costs associated with collecting quantitative fishing data (Dulvy et al. 2003). An important feature of the process is that it provides the option for a management response at any level. This is essential because most fisheries impact far more species than can ever be investigated by full stock assessment. In southern Australia, for example, full stock assessments have been undertaken on only a dozen or so species taken by trawl, gillnets, and longlines, yet hundreds of species of marine chondrichthyans, teleosts, invertebrates, mammals, birds, and reptiles are impacted. This approach will be particularly useful for developing countries where two-thirds of reported landings of chondrichthyans occurred (Bonfil 1994), resources for monitoring fishery impacts are limited (Johannes 1998), and plans of management have not been implemented.

A semi-quantitative assessment (level 2) ranked *S. megalops* at high risk given its low biological productivity and the cumulative catch susceptibility to the fishing methods. Musick (1999) proposed a productivity scale for ranking extinction risk of marine fish based on the intrinsic rate of increase, the growth coefficient (k), fecundity, age-at-maturity, and maximum age. Using either Musick's (1999) or the natural mortality (M) (present study) criteria, *S. megalops* is ranked as a low productive species. Hence, for rapid assessment at level 2, M is considered a good proxy to productivity.

Squalus megalops had moderate catch susceptibility due to cumulative effects of the different fishing methods used in southeastern Australia. Shark gillnets and Danish seines are used on the continental shelf, whereas otter trawlers operate on the upper slope throughout the SESSF and on the shelf off New South Wales, far eastern Victoria, and eastern Tasmania. When considered separately, each of the three fishing methods has low availability, but the three methods together have medium availability and therefore may increase the catch susceptibility of *S. megalops*. In addition, the availability to the otter trawl method would be high if the population is predominantly distributed on the upper continental slope. Demersal trawling may create a higher food supply by disturbing sediments and exposing prey, attracting *S. megalops* to the fishing grounds as this species of shark is an opportunistic predator that consumes a wide range of prey items (Braccini et al. 2005). When applied to a large number of species, the advantage of this approach is to allow low-risk species to be excluded from the data-intensive quantitative analysis of level 3, such that research and management efforts can be directed where most needed (Stobutzki et al. 2002; Hobday et al. 2006). Even for data-poor fisheries, where species-specific information on biological productivity or catch susceptibility is not available, this level of analysis can be applied. Information can be used from studies from other areas or on closely related species (Walker 2004) with the caution that there may be some degree of geographical variation in life-history parameters (e.g., Parsons 1993) and catch susceptibility parameters.

There are some caveats to the application of level 1 and level 2 assessments. Rejection of the methodology, particularly at level 1, will require underestimating the risk of depletion likely to occur for species with high uncertainty in score values for the different fishing impacts. However, this is minimized as the method adopts a precautionary approach, penalizing uncertainty and ranking those species for which little information is available as at risk. Risk overestimation may occur for these species at level 1, creating the need for data collection and assessment of productivity and catch susceptibility. Strong favourable opinions at levels 1 and 2 may also lead to underestimation of risk by limiting further species assessment. Therefore, objective assessment of species at these levels is critical to the performance of the methodology.

A quantitative assessment (level 3) showed that population growth of *S. megalops* is slow even under the assumption of density-dependent compensation after a fishing exploitation rate equal to the natural mortality rate. For both the best- and worst-case scenarios, the estimations of rebound potential (r_z) and population doubling time (T_D) are low even within the range reported for shark species (0.017–0.136 year^{-1} and 5.1–41.5 years, respectively) and are similar to the values reported for the spiny dogfish (*S. acanthias*) from the northwestern Atlantic (Smith et al. 1998). Population growth rate (λ) was also slow, placing *S. megalops* towards the "slow" end of the spectrum along a continuum of life-history traits of sharks (Cortés 2002). For the worst-case scenario, most simulated λ values fell below 1, suggesting population decrease even under no fishing mortality. *Squalus acanthias* and the shortspine spurdog (*S. mitsukurii*) also show λ values below 1 and would not possess the biological attributes to restore λ to its original level after moderate exploitation (Cortés 2002). For the worst-case scenario proposed for *S. megalops*, λ values below 1 would result from the negative correlation between λ and M and the positive correlation between λ and k. Within this scenario, some of the permutations of the combined M and k that can be obtained from their respective distributions (in this case high M and low k values) resulted in λ values below 1 (McAllister et al. 2001). Elasticities of juvenile and adult survival were higher than fertility elasticities, indicating that λ is more sensitive to the survival of juveniles and adults. As for *S. acanthias* and *S. mitsukurii* (Cortés 2002), for the worst-case scenario, juvenile *S. megalops* had a higher elasticity than adults, and management actions should focus on the protection of juveniles. For the best-case scenario, because of the simulated longer life span (42 years) and the larger number of adult age classes, elasticity of adults was higher for what management actions should focus on this latter group. In all, the estimated values of r_z, T_D, and λ indicate that recovery time of *S. megalops* population after fishing overexploitation is expected to be very long. Although the relative abundance of *S. megalops* has remained stable off New South Wales (Graham et al. 2001), probably because of refuge areas where ground is untrawlable (Graham 2005), this is currently the most caught by-catch shark species taken by demersal trawlers in southeastern Australia. Trends in catch per unit effort from onboard scientific observer data suggest that the population has been stable during 1992–2005 (Walker and Gason 2006). Nevertheless, the aggregating behaviour of *S. megalops* (Graham 2005), in combination with its slow growth rate (Braccini 2006) and low reproductive output (Braccini et al. 2006), makes this species potentially vulnerable to the effects of fishing. For species with similar life-history traits, such as *S. acanthias*, stock depletions have been well documented (e.g., Holden 1977). Hence, any increase in catch susceptibility through targeting, increased retention of catch, or change in gear design such as reducing mesh size of shark gillnets could quickly increase the risk of stock depletion for *S. megalops*. Conservation and management for sustainable use of *S. megalops* will require a close control of fishing mortality because of the low biological productivity of this species.

In summary, the hierarchical ecological risk assessment approach adopted in Australia allows for the effective evaluation of the effects of fishing on non-target chondrichthyan species and the identification of species at risk. Under this approach, research and management effort can be prioritised and directed to where it is most needed. The hierarchical approach allows for management response at any level as an alternative to undertaking the research required to proceed to the next level of assessment. Hence, this approach is particularly useful for fishery management organizations for the assessment of data-limited fisheries. For example, the Australian Fisheries Management Authority (AFMA) is presently applying the approach for the evaluation of 14 fisheries as the basis for determining priorities for research, fishery monitoring, and management (Hobday et al. 2006). There is no doubt about the need for management of chondrichthyans, particularly for those taken as by-catch in multispecies fisheries: the question is how to make research and management more cost-effective and priority-driven when chondrichthyan resources are being depleted and there is insufficient time or funding available for comprehensive data collection on all species.

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Appendix A

Tables A1 and A2 follow.

Table A1. Level 1 assessment of the fishing methods having a potential impact on *S. megalops*.

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
***(a)* Otter trawl and Danish seine methods**							
Capture	1	6	6	4	3	1	*S. megalops* is captured by trawl nets throughout the range of the fishery. Moderate impact on stock as there has been no long-term decline in relative abundance in one region of the fishery (Graham et al. 2001); however, for the other regions, there is no long-term relative abundance information.
Cryptic mortality	1	6	6	2	2	2	Cryptic mortality caused by escapement of animals injured from encounters with trawl nets may happen but it is considered to have a minor impact on the stock. Certainty low because of difficulties in measuring this impact.
Gear loss	1	6	6	1	1	1	Trawl net loss is a rare event because of their high price, creating a high incentive not to loose them and to retrieve them.

Table A1 (*continued*).

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
Species translocation	1	6	6	1	1	1	Invertebrate and vertebrate species caught in trawl nets can be translocated up to several miles between shots but it is unlikely to have a measurable impact on the stock through habitat modification.
On-board processing and catch discarding	1	6	6	3	3	2	Moderate to large quantities of organisms are discarded in trawling operations. This practice can attract opportunistic species, such as *S. megalops* (Braccini et al. 2005), increasing the probability of being taken by the gear. However, the extent of this impact is uncertain because of a lack of data.
Provisioning	0					1	Provisioning does not occur in this method.
Pollution	1	6	6	2	1	1	Chemical or physical pollutants might have minor risks as this hazard only affects a small area and *S. megalops* is a mobile species with an avoidance ability > scale of the hazard. Impact on stock is considered negligible.
(*b*) Shark gillnet method							
Capture	1	6	6	3	4	1	Shark gillnets (6–6.5 inch mesh size) are designed to target larger-sized species (e.g., *M. antarcticus*), so only large female *S. megalops* are taken throughout the range of the fishery (Walker et al. 2005). Selective removal of significant numbers of large females could have a major impact on the stock.
Cryptic mortality	1	6	6	2	2	2	Refer to part *a*.
Gear loss	1	6	6	1	1	1	Refer to part *a*.
Species translocation	1	6	6	1	1	1	Refer to part *a*.
On-board processing and catch discarding	1	6	6	3	3	2	Refer to part *a*.
Provisioning	0					1	Refer to part *a*.
Pollution	1	6	6	2	1	1	Refer to part *a*.
(*c*) Automatic longline method							
Capture	1	6	6	3	3	2	This fishing method is used across a broad spatial and temporal scale but only in deepwater (continental slope) where *S. megalops* is not very abundant; hence, the impact on the stock is considered moderate.
Cryptic mortality	1	6	6	2	2	2	Refer to part *a*.
Gear loss	1	6	6	1	1	1	Refer to part *a*.
Species translocation	1	6	6	1	1	1	Refer to part *a*.

Table A1 (*concluded*).

Fishing activity	Presence	Spatial scale	Temporal scale	Intensity	Consequence	Certainty	Rationale
On-board processing and catch discarding	1	6	6	2	2	1	Discards in this fishery are minimal, having a minor effect on the stock.
Provisioning	1	6	6	2	2	1	The most commonly used bait is squid, which is harvested at low levels with minor consequence for the stock of squid and, hence, minor indirect effect on *S. megalops* stock.
Pollution	1	6	6	2	1	1	Refer to part *a*.

Note: Presence score: 1, present; 2, absent. Certainty score: 1, certain (data exist and considered sound); 2, uncertain (no data or considered poor or conflicting; see Table 2 for score value description).

Table A2. Catch susceptibility for otter trawl and Danish seine method, shark gillnet method, and automatic longline method.

	Parameter					
Fishing method	Av	Ec	Se	Pc	Cs	Rationale
Otter trawl and Danish seine	L–Mo	H	H	H	L–Mo	This method is confined to the continental shelf and upper slope overlapping in part with the *S. megalops* spatial distribution. Encounterability is high because of depth distribution of gear and species. Selectivity is high given uncertainty in selectivity of trawl nets. Post-capture mortality is also high because of trauma caused inside the net.
Shark gillnet	Mo	H	L	Mo	L	This method is confined to the continental shelf, mostly inside the 120–150 m isobath, with moderate overlap with the *S. megalops* spatial distribution. Encounterability is high because of depth distribution of gear and species. Selectivity is low because of the 6–6.5 inch mesh size of the gillnet (see Walker et al. 2005, table 6).
Automatic longline	L	H	H	Mo	L	This method is confined to the continental slope with very low overlap with the *S. megalops* spatial distribution. Encounterability is high because of depth distribution of gear and species as *S. megalops* is likely to take the baited hook, given its opportunistic feeding behaviour. Selectivity is high given that hook size does not affect catch (see Walker et al. 2005).

Note: Risk categories of availability (Av), encounterability (Ec), selectivity (Se), post-capture mortality (Pc), and catch susceptibility (Cs) are L (low, 0.33), Mo (moderate, 0.66), and H (high, 1.00).

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Short communication

Total and partial length–length, mass–mass and mass–length relationships for the piked spurdog (*Squalus megalops*) in south-eastern Australia

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Abstract

Common commercial fishing practices of eviscerating, beheading and finning sharks create the need for using conversion factors from partial lengths to total length and from partial masses to total mass. In the present paper, these conversion factors were calculated for *Squalus megalops*. In addition, total and partial length–length and mass–length relationships of male and female *S. megalops* were compared using different ranges of size. There was no effect of size range on measurements reflecting only somatic growth (fork and carcass lengths; carcass, pectoral fin and caudal fin masses) but for variables reflecting somatic and reproductive growth (total and liver masses), different outcomes can be expected when different ranges of size are compared.

Keywords: Conversion factors; *Squalus megalops*; Elasmobranchs; Australia

1. Introduction

Fisheries taking sharks are common throughout the world. Given that commercial shark species are normally beheaded, eviscerated and landed in one of the two forms: with fins attached (carcass) or without fins attached (trimmed carcass), only partial lengths and masses can be recorded after landing (FAO, 2000). Furthermore, due to increase in worldwide demand for shark fins, in many fisheries only the fins are retained whereas the rest of the animal is discarded. Due to these fishing practices, relationships between partial lengths and total length and between partial masses and total mass of shark are needed to determine the length and mass composition of captured sharks. Therefore, conversion to live weight and length equivalent units using appropriate conversion factors is an essential requirement for fisheries monitoring programmes and stock assessments.

Size relationships and size conversion factors have several biological applications and are commonly used in fishery management. Size relationships, particularly total mass–total length relationship, are commonly reported in biological studies of sharks (e.g. Stevens and McLoughlin, 1991; Kohler et al., 1995). Many studies test for differences between sexes in these relationships; in some cases, significant differences are found (e.g. Chiaramonte and Pettovello, 2000; Walker, 2005), whereas other studies show no differences (e.g. Bridge et al., 1998; Francis and Stevens, 2000). Many species of sharks exhibit sexual dimorphism in maximum size, females being larger and heavier than males (e.g. Cortés, 2000). For these species, size relationship comparisons are thus made between groups of different ranges of size so similarities or differences in these relationships may be an artefact of comparing smaller individuals (males) with larger individuals (females).

In the present study, length–length and mass–length relationships of male and female piked spurdogs (*Squalus megalops*), an abundant shark of southern Australia (Graham et al., 2001), were compared using different ranges of size. In

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Table 1
Conversion factors derived from geometric mean regressions

Variables		N	$b \pm$ S.E.	$a \pm$ S.E.
X	Y			
(a)				
Fork length	Total length	547	1.138 ± 0.005	5.736 ± 1.857
Carcass length	Total length	490	1.587 ± 0.017	26.764 ± 4.419
Carcass mass	Total mass	851	1.939 ± 0.011	-58.518 ± 3.537
Pectoral fin mass	Total mass	351	64.437 ± 0.962	-87.998 ± 9.119
Caudal fin mass	Total mass	352	82.529 ± 0.948	-136.357 ± 7.562
(b)				
Total length	Fork length	547	0.878 ± 0.004	-4.972 ± 1.651
Total length	Carcass length	490	0.630 ± 0.007	-16.901 ± 2.959
Total mass	Carcass mass	851	0.516 ± 0.003	30.230 ± 1.676
Total mass	Pectoral fin mass	351	$0.016 \pm 2.31 \times 10^{-4}$	1.367 ± 0.123
Total mass	Caudal fin mass	352	$0.013 \pm 1.43 \times 10^{-4}$	1.467 ± 0.076

Estimated parameters for converting (a) partial lengths and partial masses to total length and total mass and (b) total length and total mass to partial lengths and partial masses. Values for parameters (and standard error) derived from the equation $Y = a + b\,X$. a and b are parameters and N is sample size.

addition, due to the common fishing practice of eviscerating, beheading and finning sharks, conversion factors from partial lengths and partial masses to total length and total mass were determined.

2. Materials and methods

Male and female *S. megalops* were collected from the by-catch of shark and demersal trawl fishery vessels operating in the Australian Southern and Eastern Scalefish and Shark Fishery during October 2002–April 2004. Total (TL), fork (FL) and carcass (CL) lengths were measured to the nearest millimetre. Fork length was measured from the tip of the snout to the caudal fork and CL was measured from the fifth gill-slit to the precaudal pit. Total (TM), carcass (CM), liver (LM), pectoral fins (PFM) and caudal fin (CFM) masses were recorded to the nearest gram. All length and mass measures were recorded in the laboratory. Differences between sexes were tested by Student *t*-test on the slopes and intercepts of the linear regression of FL and CL against TL and the linear regression of ln (TM), ln (CM), ln (LM) ln (PFM), and ln (CFM) against ln (TL) or ln (CL) (Kleinbaum et al., 1988). A factor is used to correct for biases caused by natural logarithmic transformation (Beauchamp and Olson, 1973).

S. megalops showed sexual dimorphism in maximum size, ranging from 274 to 470 mm TL (86–465 g TM) and 270–635 mm TL (84–1411 g TM) for males and females, respectively. Hence, samples of different ranges of size were selected for statistical comparisons. The following groups were compared: males ($n = 207$), all females ($n = 721$) and small females (≤ 470 mm TL, $n = 297$). Geometric mean regressions (Ricker, 1973) were used to determine conversion factors from partial lengths and partial masses to total length and total mass and from total length and total mass to partial lengths and partial masses.

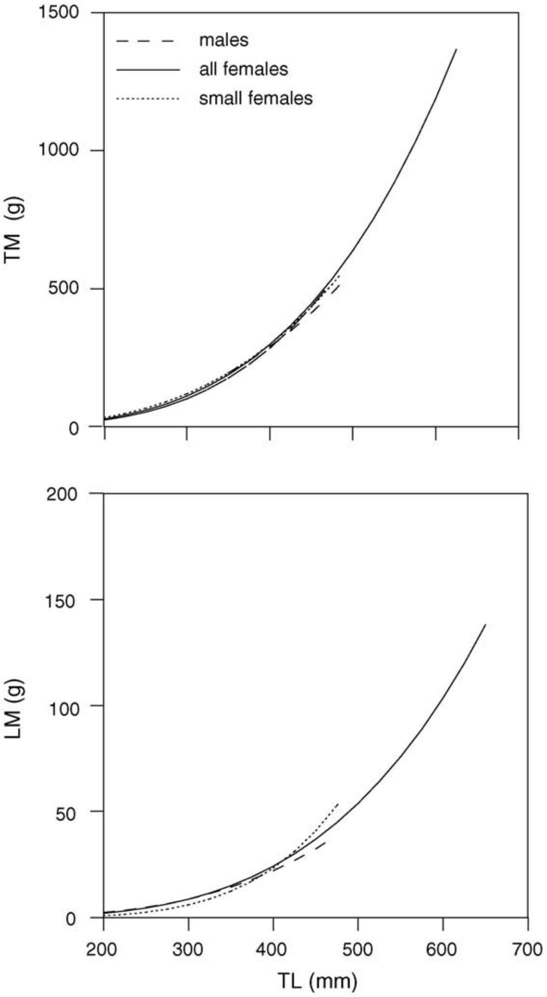

Fig. 1. Predicted relationship between total mass (TM) and total length (TL) and between liver mass (LM) and TL for males, all females and small females. Values for parameters are given in Table 2.

Table 2
Estimated parameters (and standard error) for the relationship between total mass (TM) and total length (TL) and between liver mass (LM) and total length (TL) for males, all females and small females, derived from the equation $TM = a\,c\,TL^b$ and $LM = a\,c\,TL^b$

Shark group	*a* (S.E. range)	*b* (±S.E.)	*c*	*N*	R^2
TM–TL					
Males	2.15 (1.44–3.20) × 10^{-6}	3.124 (0.07)	1.003	205	0.91
All females	2.54 (2.18–2.96) × 10^{-7}	3.482 (0.03)	1.005	699	0.97
Small females	8.09 (5.76–11.40) × 10^{-7}	3.290 (0.06)	1.006	297	0.92
LM–TL					
Males	7.15 (1.34–38.20) × 10^{-8}	3.257 (0.28)	1.034	196	0.41
All females	1.05 (0.59–1.87) × 10^{-8}	3.587 (0.09)	1.065	679	0.69
Small females	1.03 (0.41–2.63) × 10^{-11}	4.743 (0.16)	1.031	287	0.76

a and *b* are parameters, *c* is the Beauchamp and Olson (1973) correction factor for logarithmic transformation, *N* is sample size and R^2 is square of correlation coefficient.

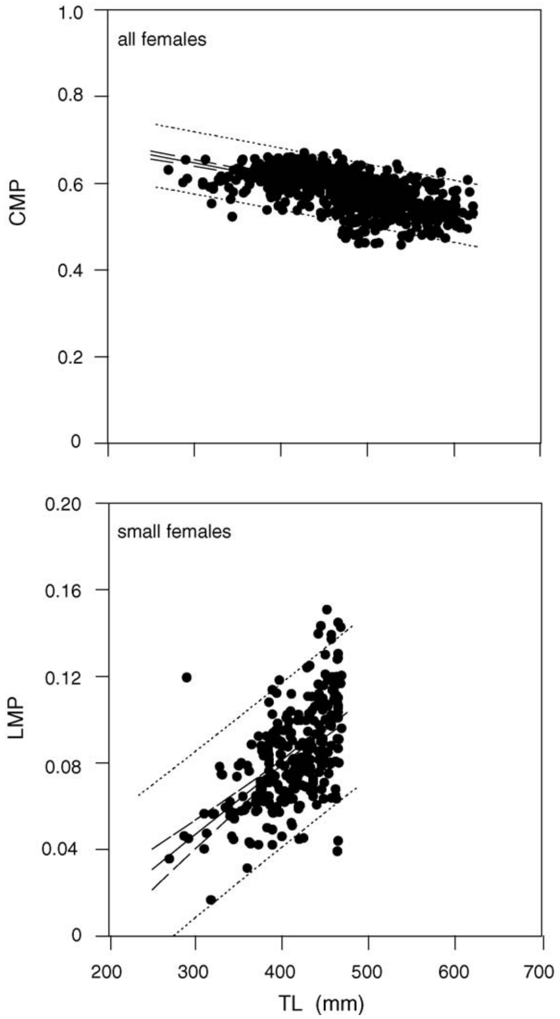

Fig. 2. Relationship between carcass mass as a proportion of total mass (CMP) and total length (TL) for all females and between liver mass as a proportion of total mass (LMP) and TL for small females with 95% confidence intervals around the mean (– – –) and 95% predicted intervals around the data (· · ·). All females: CMP = 0.758 (0.01) −3.723 (0.21) × 10^{-4} TL, *n* = 660, $R^2 = 0.32$, and small females: LMP = −0.049 (0.01) + 3.211 (0.28) × 10^{-4} TL, *n* = 279, $R^2 = 0.32$.

3. Results

There were no significant differences in the FL–TL, CL–TL, CM–TL, PFM–TL, CFM–TL and CM–CL relationships between males and all females and between males and small females (*t*-test, $P > 0.05$ for comparisons of slopes and intercepts). Therefore, sexes and sizes were pooled for calculation of conversion factors, shown in Table 1. The conversion factors estimated are applicable to the size range analysed (270–635 mm TL), which covers most of the population size range, with the exception of neonates (TL < 270 mm).

There were significant differences in the TM–TL relationship between males and all females (*t*-test, d.f. = 902, $t = 5.06$, $P < 0.05$ for comparison of slopes and $t = 5.01$, $P < 0.05$ for comparison of intercepts, Fig. 1). However, when animals of the same size range were compared (males and small females), no differences were detected (*t*-test, d.f. = 500, $t = 1.78$, $P > 0.05$ for comparison of slopes and $t = 1.74$, $P > 0.05$ for comparison of intercepts, Fig. 1). There were no differences in the LM–TL relationship between males and all females (*t*-test, d.f. = 873, $t = 0.89$, $P > 0.05$ for comparison of slopes and $t = 0.86$, $P > 0.05$ for comparison of intercepts, Fig. 1), but significant differences were detected between males and small females (*t*-test, d.f. = 481, $t = 4.51$, $P < 0.05$ for comparison of slopes and $t = 4.47$, $P < 0.05$ for comparison of intercepts, Fig. 1). To standardize for the effects of size, CM and LM were expressed as a proportion of TM. Carcass mass expressed as a proportion of TM (CMP) decreased with TL for all females (Fig. 2), whereas the CMP–TL relationship showed no trend for males and a slight decrease for small females (not shown). Liver mass expressed as a proportion of TM (LMP) increased with TL for small females (Fig. 2). For males and all females, the LMP–TL relationship showed no trend (not shown).

4. Discussion

There were no sex or size effects in the FL–TL, CL–TL, CM–TL, PFM–TL, CFM–TL and CM–CL relationships.

These length and mass measures reflect structural size and somatic growth with little trade-off between somatic and reproductive growth. Otherwise, the relatively larger increase in reproductive tissue experienced by adult female sharks (e.g. Yano, 1995) would be coupled with a decrease in their somatic tissue, particularly carcass mass, expecting differences in the CM–TL and CM–CL relationships of all females compared with males or small females. Hence, for measurements that only reflect somatic growth (e.g. partial lengths, fin masses), comparing different ranges of size had no effect on the relationships between these variables and TL.

Total mass and LM reflect somatic growth and reproductive investment. As the costs of reproduction are different between males and females (Stearns, 1992), different outcomes can be expected when testing for differences between sexes if different ranges of size are compared. This is of particular concern for species that exhibit sex and size segregation, such as *S. megalops* (Graham, 2005), for which the full size range of the population may not be adequately represented. Male and small female *S. megalops* had a similar TM–TL relationship, but this relationship was different from the TM–TL relationship of all females. Thus, if sampling is biased towards particular size-classes due to size-selectivity of the sampling gear or size or sex segregation of sharks, comparisons between sexes may not reflect real differences or similarities in the TM–TL relationship. Hence, given the opportunistic sampling nature of most biological studies of sharks and the small sample size of many studies, care must be taken when determining mass–length relationships. If the size range is not fully represented, mass–length relationships may be biased, affecting predictions of population assessments that use these relationships as inputs to the models. Likewise, the LM–TL relationship of *S. megalops* differed between the sexes depending on the ranges of size compared. For some squalid sharks (Yano, 1995; Clarke et al., 2001) and other elasmobranchs (e.g. Craik, 1978), size of liver varies with reproductive stage, being relatively smaller for pregnant females. Liver lipid reserves are used for vitellogenesis (Craik, 1978); hence, an increase in liver lipids and liver mass is expected for females entering first maturation. This was reflected in the larger slope of the LM–TL relationship and the increase in LMP with TL for small females. This pattern was obscured when small and large females were pooled as no trend was observed for this relationship when using all females and also no differences were found in the LM–TL relationship of males and all females. Therefore, the relationships between variables that reflect somatic growth and reproductive dynamics and TL are affected by the ranges of size used.

Most life history parameters used in shark stock and demographic assessments are determined as a function of TL or TM (e.g. maturity and maternity ogives, fecundity). Also some shark fisheries use minimum and maximum size limits to regulate the catch. However, commercial shark species are normally beheaded, eviscerated and finned so only the mass and length of the carcass or the mass of the fins can be recorded after landing. It is, therefore, essential to determine how these partial lengths and masses can be converted to TL or TM (FAO, 2000). When measurements reflect only somatic growth, conversion factors to TL or TM can be determined pooling sexes and sizes, but for measurements that reflect both somatic and reproductive growth, conversion factors should be determined for sexes and sizes separately. Although many studies provide TM–TL relationships, few present conversion factors to allow calculating TL or TM from partial length or partial mass measures. Geometric mean regressions were used to determine conversion factors for several length–length and mass–mass relationships for *S. megalops*. These conversion factors are essential for assessment of this species. Given the depletion of many of the harvested species of sharks and a decline in abundance of most other shark species in southern Australia (Graham et al., 2001), *S. megalops* will inevitably become a more sought after species.

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Nota de Investigación/Research Note

Notas sobre la estructura poblacional del tiburón *Squalus megalops* en el sureste de Australia

Notes on the population structure of the piked spurdog (*Squalus megalops*) in southeastern Australia

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Resumen

Un muestreo oportunista reveló una estructura poblacional compleja para *Squalus megalops* en el sureste de Australia. Se analizaron un total de 929 tiburones. La razón de sexos estuvo sesgada hacia las hembras y se observó dimorfismo sexual en la talla, alcanzando las hembras una mayor talla máxima que los machos. El análisis individual de algunos lances de pesca mostró que *S. megalops* tiene una estructura poblacional compleja y que presenta segregación por sexo, talla y condición reproductiva. Las hembras y los machos de talla pequeña se segregaron de las hembras grandes, y las hembras en su primer año de preñez parecieran separarse de las que estaban en su segundo año de preñez.

Palabras clave: *Squalus megalops*, estructura poblacional, dimorfismo en talla.

Abstract

Opportunistic sampling suggested a complex population structure for *Squalus megalops* in southeastern Australia. A total of 929 sharks were analyzed. The sex ratio was biased towards females and there was sexual size dimorphism, with females attaining a larger maximum size than males. Individual analysis of selected fishing shots suggested that *S. megalops* had a complex population structure, and was segregated by sex, size and breeding condition. Small females and males segregated from large females. In addition, large females in the first year of pregnancy seemed to be separated from those in the second year of pregnancy.

Key words: *Squalus megalops*, population structure, size dimorphism.

Introducción

La mayoría de las especies de tiburones pequeños del orden Squaliformes tienen estructuras poblacionales complejas. Una característica común de este grupo de peces es la segregación temporal y espacial por sexo, talla y condición de madurez. Se ha observado que las hembras preñadas y en la fase de ovulación de *Centroscymnus owstoni* se separan de los especímenes inmaduros (Yano y Tanaka 1988). Existen reportes sobre la segregación por talla y sexo de *Centroscyllium fabricii* (Yano 1995), *Etmopterus granulosus* (Wetherbee 1996), *Centrophorus squamosus* y *Centroscymnus coelolepis* (Clarke 2000), y *Deania calcea* (Clark y King 1989, Clarke *et al.* 2002). Entre las especies del género *Squalus*, *S. acanthias* L muestra una compleja estructura problacional relacionada con su ciclo reproductivo (e.g., Ketchen 1986). Enfrente de Nueva Zelanda, el alumbramiento, la ovulación y el apareamiento se producen en aguas profundas, mientras que las hembras preñadas permanecen en aguas someras durante su primer año de gestación, antes de migrar de nuevo a aguas profundas durante su segundo año (Hanchet 1988).

Introduction

Most dogfish species (Squaliformes) have complex population structures. Segregation in time and space by sex, size and mature condition is a common feature of this group. Pregnant and ovulating females of *Centroscymnus owstoni* segregate from immature specimens (Yano and Tanaka 1988). Size and sexual segregation have been reported for *Centroscyllium fabricii* (Yano 1995), *Etmopterus granulosus* (Wetherbee 1996), *Centrophorus squamosus* and *Centroscymnus coelolepis* (Clarke 2000), and *Deania calcea* (Clark and King 1989, Clarke *et al.* 2002). Among *Squalus* species, *S. acanthias* L exhibits a complex population structure related to its reproductive cycle (e.g., Ketchen 1986). Off New Zealand, parturition, ovulation and mating occur in deep water, whereas pregnant females spend the first year of gestation in shallow waters before migrating back to deep water during the second year of pregnancy (Hanchet 1988).

A complex size structure has also been reported for *Squalus megalops* (Macleay 1881) (fig. 1). In South Africa, *S.* cf. *megalops* forms large schools often segregated by sex and size (Compagno 1990). In New South Wales, southeast coast of

Squalus megalops (Macleay 1881) (fig. 1) es otra especie que presenta una estructura poblacional compleja. En Sudáfrica, *S.* cf. *megalops* forma cardúmenes grandes, frecuentemente segregados por sexo y talla (Compagno 1990). En las costas de Nueva Gales del Sur, al sureste de Australia, las hembras de talla grande se separan de los machos y juveniles, agrupándose en aguas más profundas y en regiones diferentes (Graham 2005). En Australia, particularmente en el sur, se han agotado muchas de las especies de tiburón capturadas y la abundancia de la mayoría de las otras especies de tiburón ha disminuido (Graham *et al.* 2001). La abundancia natural de *S. megalops* aún es alta (Bulman *et al.* 2001, Graham *et al.* 2001), por lo que es de esperarse que aumente el interés en esta especie. Considerando que *S. megalops* ya compone la mayor parte de la captura comercial de tiburones pequeños en el sureste de Australia (Daley *et al.* 2002), es necesario un mejor conocimiento de su estructura poblacional.

Este estudio tiene por objeto determinar la estructura poblacional de *S. megalops* en el sureste de Australia. Debido a la complejidad de los patrones de segregación que presentan las especies del género *Squalus*, se hace énfasis en la separación entre sexos, tallas y condiciones reproductivas.

Material y métodos

Se recolectaron especímenes de *S. megalops* de manera oportunista entre la captura incidental de las embarcaciones de pesca con red de enmalle para tiburón y red de arrastre demersal que operan en la pesquería de tiburón y peces de escama en el sur y este de Australia. Las muestras se recolectaron entre octubre de 2002 y abril de 2004, principalmente de las localidades de Robe, Lakes Entrance y Ulladulla (fig. 2). Se empleó de 4 a 8 horas una red de enmalle para tiburón, de monofilamento, luz de malla de 16.5 cm, ~4000 m de longitud y 2.4 m de profundidad, durante la noche y el día. Los aparejos de arrastre de fondo utilizados fueron la red de arrastre de puertas y la red danesa, el primero con una relinga superior de 24–50 m y luz de malla estirada en el copo de 90 mm y el segundo con una relinga superior de 30–59 m y luz de malla estirada en el copo de 38 mm. Los arrastres se realizaron por 3–4 horas durante la noche y el día. La profundidad de pesca fue de entre 21 y 238m y varió según la localidad y el arte de pesca. Las longitudes totales (LT) de *S. megalops* fueron medidas al milímetro más cercano y la condición reproductiva de los machos y las hembras se determinó siguiendo las recomendaciones de Braccini *et al.* (2006).

Se determinaron la razón de sexos y la distribución de frecuencias de longitud para la totalidad de la muestra y por lance de pesca cuando se contaba con los datos de profundidad y el tamaño de muestra por lance fue ≥10. Para la muestra total se utilizaron la prueba chi-cuadrada con la corrección de continuidad de Yates y la prueba de Kolmogorov-Smirnov (KS) (Zar 1999) para probar si existían diferencias en la razón de sexos y la distribución de frecuencia de longitud de machos y hembras, respectivamente.

Australia, large females segregate from males and juveniles, aggregating in deeper waters and different regions (Graham 2005). In Australia, particularly in the south, many of the harvested species of sharks have been depleted and the abundance of most other shark species has declined (Graham *et al.* 2001). *Squalus megalops* has a high natural abundance (Bulman *et al.* 2001, Graham *et al.* 2001) and so is likely to become a more sought after species. As *S. megalops* already comprises most of the marketed catch of dogfish in southeastern Australia (Daley *et al.* 2002), a better understanding of the population structure of this species is needed.

The aim of the present study is to determine the population structure of *S. megalops* in southeastern Australia. Owing to complex segregation patterns found in *Squalus* species, emphasis is put on separation between sexes, sizes and breeding condition.

Material and methods

Specimens of *S. megalops* were collected opportunistically from the by-catch of shark gillnet and demersal trawl fishing vessels operating in the Australian Southern and Eastern Scalefish and Shark Fishery between October 2002 and April 2004. Samples were mainly collected from Robe, Lakes Entrance and Ulladulla (fig. 2). Shark gillnet fishing gear consisted of 16.5cm monofilament mesh-size, ~4000 m long and 2.4 m deep, deployed for 4–8 hours during the night and day. Demersal trawl fishing gear consisted of otter trawl or Danish seine nets. Otter trawl nets had a headline length of 24–50 m, with a stretched codend mesh size of 90 mm, and Danish seine nets had a headrope length of 30–59 m, with a stretched codend mesh size of 38 mm. Trawling operations lasted for 3–4 hours during the night and day. Fishing depth was between 21 and 238m, and varied with location and fishing gear. *Squalus megalops* total lengths (TL) were measured to the nearest millimetre. The reproductive condition of males and females was determined following Braccini *et al.* (2006).

Sex ratio and length-frequency distribution were determined for the entire sample and per fishing shot when depth information was available and sample size per shot was ≥10. For the entire sample, a chi-square test with Yates' continuity correction and a Kolmogorov-Smirnov test (KS) (Zar 1999) were used to test for differences in the sex ratio and the length-frequency distribution of males and females, respectively.

Results

Data from a total of 929 sharks were analyzed. For the entire sample, the sex ratio (males:females) was significantly biased towards females (1:3.49, $\chi^2 = 284.39$, d.f. = 1, $P < 0.001$). By fishing gear, the sex ratio was also biased towards females (1:25.34, $\chi^2 = 133.07$, d.f. = 1, $P < 0.001$, for shark gillnets; and 1:2.83, $\chi^2 = 175.64$, d.f. = 1, $P < 0.001$, for demersal trawl nets). Size ranged from 274 to 470 mm TL for males and from 270 to 635 mm TL for females. There was sexual

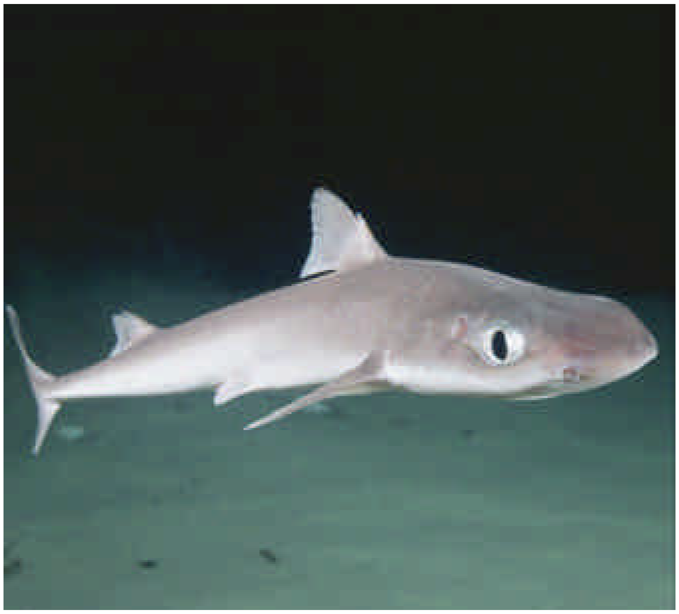

Figura 1. Squalus megalops de las costas de Nueva Gales del Sur, Australia.
Figure 1. *Squalus megalops* of the coasts of New South Wales, Australia.

Resultados

Se analizaron datos de un total de 929 tiburones. Para la totalidad de la muestra, la razón de sexos (macho:hembra) estuvo muy sesgada hacia las hembras (1:3.49, $\chi^2 = 284.39$, g.l.=1, $P < 0.001$). Por arte de pesca, la razón de sexos también presentó un sesgo hacia las hembras (1:25.34, $\chi^2 = 133.07$, g.l. = 1, $P < 0.001$, para las redes de enmalle; y 1:2.83, $\chi^2 = 175.64$, g.l. = 1, $P < 0.001$, para las redes de arrastre de fondo). La talla varió de 274 a 470 mm LT para los machos y de 270 a 635 mm LT para las hembras. Se observó dimorfismo sexual en la talla máxima, siendo la LT media (±EE) de machos de 404(±2) mm, mientras que la de hembras fue de 480(±3) mm. Las distribuciones de frecuencias de longitud de los machos y las hembras (fig. 3a) fueron significativamente diferentes (KS, $d_{\mathrm{MAX}} = 0.685$, $n_{\mathrm{machos}} = 207$, $n_{\mathrm{hembras}} = 722$, $P < 0.001$). Las redes de enmalle capturaron principalment hembras de talla grande (fig. 3b), por lo que las muestras recolectadas con éstas fueron excluidas del análisis de la estructura poblacional ya que probablemente no se muestrearon hembras y machos pequeños debido a la posible selectividad de talla de este aparejo. En vista de que la red de arrastre de puertas y la red danesa capturaron ambos sexos con mayor intervalo de tallas (fig. 3c, d), estas muestras sí se usaron para tal análisis.

Los análisis de la razón de sexos y las distribuciones de frecuencias de longitud de algunos arrastres seleccionados (n =18) indicaron que *S. megalops* presenta un patrón de agrupación complejo. En algunos lances, machos y hembras pequeñas (<460 mm LT) fueron capturados juntos (fig. 4a; tabla 1, lances 146, 155), mientras que en otros, se capturaron principalmente hembras inmaduras (fig. 4b; tabla 1, lance 205)

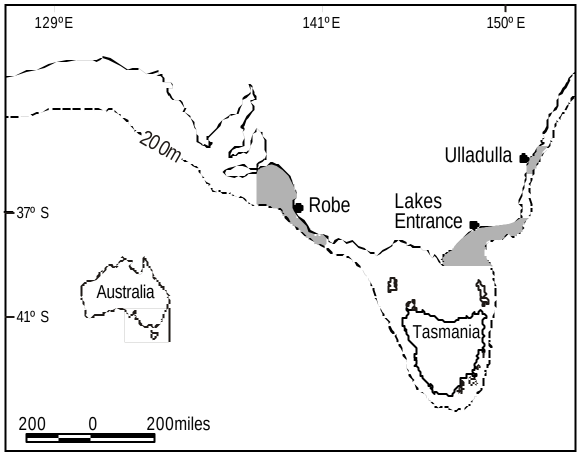

Figura 2. Mapa del área de estudio en el sureste de Australia.
Figure 2. Map of the sampling area in southeastern Australia.

dimorphism in maximum size: mean TL (±SE) of males was 404 (±2) mm, whereas mean TL of females was 480 (±3) mm. Length-frequency distributions (fig. 3a) were significantly different between males and females (KS, $d_{\mathrm{MAX}} = 0.685$, $n_{\mathrm{males}} = 207$, $n_{\mathrm{females}} = 722$, $P < 0.001$). Shark gillnets mainly captured large females (fig. 3b), so samples collected with this fishing method were excluded from the analysis of population structure since small females and males may have not been sampled by the gillnet due to possible size-selectivity of this fishing gear. Otter trawl and Danish seine nets caught both sexes with a broader range of sizes (fig. 3c, d), so these samples were used for the analysis of population structure.

Analyses of sex ratio and length-frequency distributions of selected trawl fishing shots ($n = 18$) suggested that *S. megalops* had a complex schooling pattern. In some cases, males and small females (<460 mm TL) were trawled together (fig. 4a; table 1, shots 146, 155), but in other shots, mainly small immature females (fig. 4b; table 1, shot 205) or large females were captured (fig. 4c; table 1, shots 497, 509, 540). Among large females, those in the first year of pregnancy tended to be separated from those in the second year of pregnancy (table 1, shots 497, 509, 540). In one shot, a school of large males was caught (fig. 4d; table 1, shot 491).

Discussion

The present study provides evidence of a complex population structure for *S. megalops* in southeastern Australia. Although the opportunistic nature of the sampling design did not allow for the effects of time, region, depth or sampling gear to be rigorously tested, individual analysis of selected fishing shots suggests that *S. megalops* segregates by sex, size and breeding condition. Sexual and size segregation is a common characteristic of many shark species, where juveniles, adult males and adult females separate into different groups (Springer 1967). Male and small female *S. megalops* were caught together and did not occur with large females.

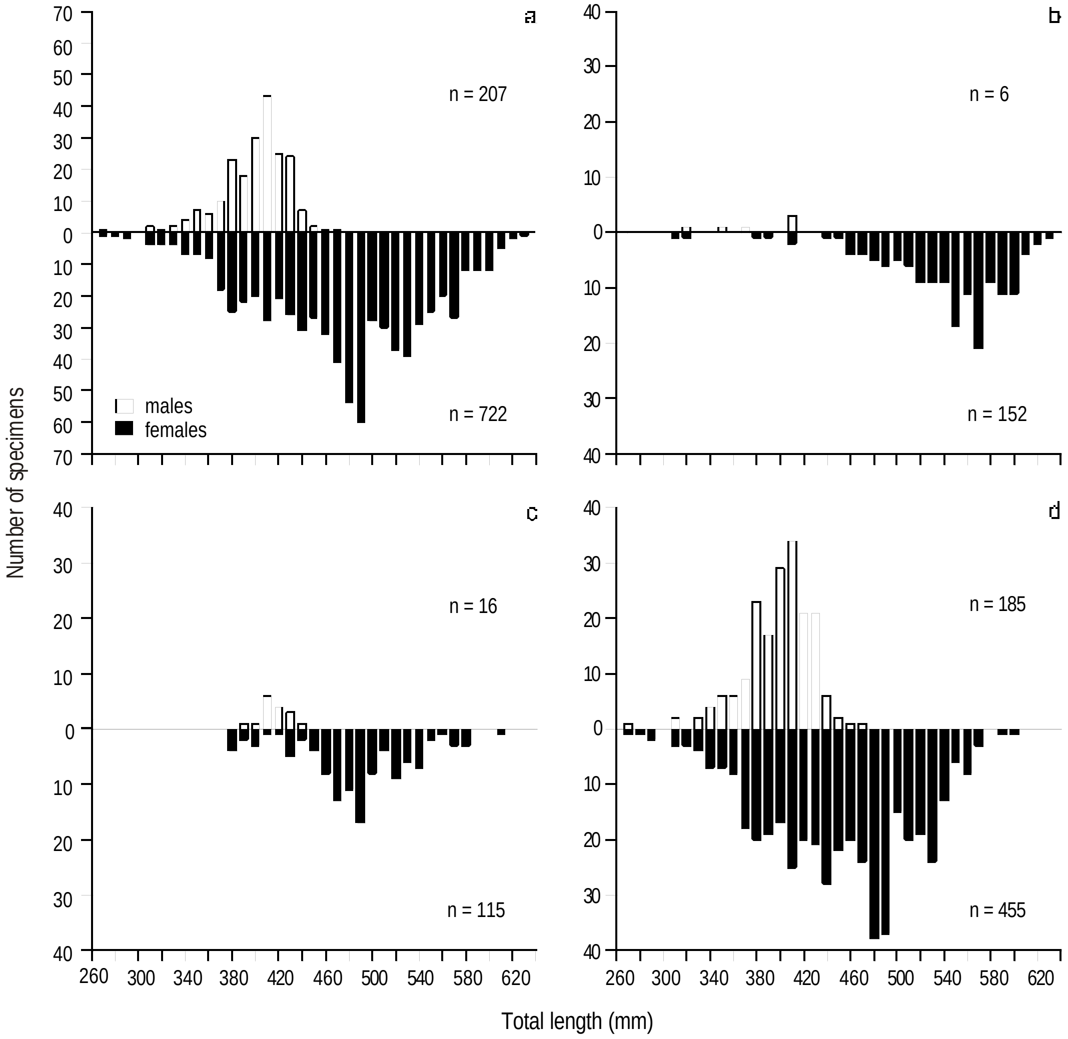

Figura 3. Distribuciones de frecuencias de longitud de *Squalus megalops* para la totalidad de la muestra (**a**) y por arte de pesca: (**b**) red de enmalle para tiburón, (**c**) red de arrastre con puertas y (**d**) red danesa.

Figure 3. Length-frequency distributions of *Squalus megalops* for the entire sample (**a**) and by fishing gear: (**b**) shark gillnet, (**c**) otter trawl net, and (**d**) Danish seine net.

o de talla grande (fig. 4c; tabla 1, lances 497, 509, 540). Entrelas hembras grandes, las que se encontraban en su primer año de preñez tendían a separarse de las que estaban en su segundo año (tabla 1, lances 497, 509, 540). En un lance se capturó un cardumen de machos de talla grande (fig. 4d; tabla1, lance 491).

Discusión

El presente estudio evidencia una estructura poblacional compleja para *S. megalops* en el sureste de Australia. A pesar de que la naturaleza oportunista del diseño de muestreo no permitió comprobar rigurosamente los efectos del tiempo, la región, la profundidad o el arte de pesca, el análisis individual de algunos lances de pesca indica que *S. megalops* se segrega por sexo, talla y condición reproductiva. La segregación por sexo y talla es una característica común de muchas especies de

Furthermore, in one of the shots, a school of only large mature males was collected and on other occasions, schools of only large females were captured. Graham (2005) reported a similar pattern off New South Wales, where large females and males occur in different regions and depths. In addition, large females in the first year of pregnancy seemed to be separated from those in the second year of pregnancy. Similarly, large female *S. acanthias* segregate by breeding condition. Pregnant females spend the first year of pregnancy in shallow waters, perhaps due to warmer water requirements for early embryo development, and migrate to deeper offshore waters during the second year of pregnancy (Hanchet 1988). Our results, although fragmentary, also suggest that female *S. megalops* in the second year of pregnancy occur in deeper waters than females in the first year of pregnancy.

Female *S. megalops* attained larger sizes than males. Sexual size dimorphism is frequently observed in sharks and it

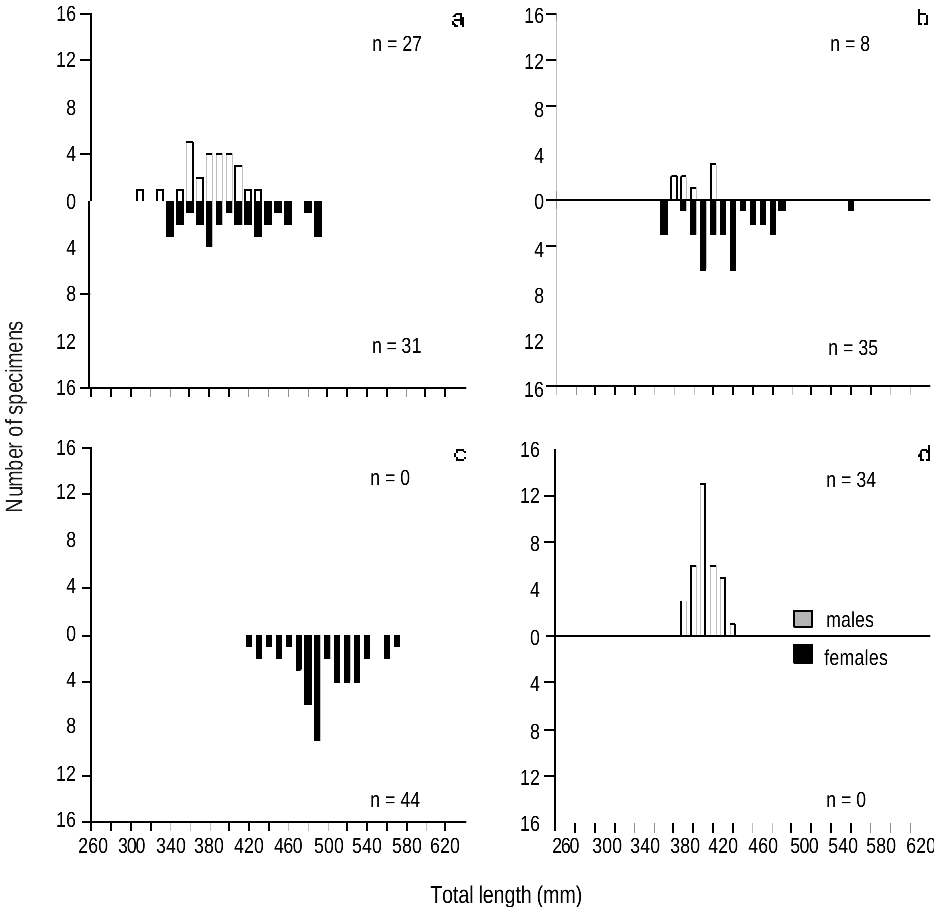

Figura 4. Distribuciones de frecuencias de longitud de algunos de los lances de pesca seleccionados: (**a**) 146 (Lakes Entrance, red danesa, verano), (**b**) 205 (Lakes Entrance, red danesa, otoño), (**c**) 509 (Lakes Entrance, red danesa, verano) y (**d**) 491 (Queenscliff, red danesa, verano)

Figure 4. Length-frequency distributions of some of the selected fishing shots: (**a**) 146 (Lakes Entrance, Danish seine net, summer), (**b**) 205 (Lakes Entrance, Danish seine net, autumn), **(c)** 509 (Lakes Entrance, Danish seine net, summer), and (**d**) 491 (Queenscliff, Danish seine net, summer).

Tabla 1. Detalles de los lances de pesca seleccionados mostrando el número de machos inmaduros (I) y maduros (M), así como el número de hembras inmaduras (I), en su primer año de preñez (Year 1), en su segundo año de preñez (Year 2) y en ovulación y postparto (O & P-p). Artes de pesca: red danesa (Ds) y red de arrastre (Tn).
Table 1. Sample details for selected fishing shots showing the number of immature (I) and mature (M) males, and the number of immature (I), first year of pregnancy (Year 1), second year of pregnancy (Year 2) and ovulating and post-partum (O & P-p) females. Gear: Danish seine net (Ds) and trawl net (Tn).

Shot	Location	Month	Gear	Mean depth (m)	Number						Sex ratio (m:f)	Mean size (±SE)	
					Male		Female					Male	Female
					I	M	I	Year 1	Year 2	O & P-p			
146	Lakes Entrance	February	Ds	73.0	22	5	28	2	1	0	1:1.1	386 (5)	421 (8)
509	Lakes Entrance	February	Ds	68.5	0	0	10	29	4	1	–	–	500 (5)
155	Lakes Entrance	March	Ds	38.0	3	6	7	2	0	2	1:1.2	434 (4)	476 (12)
205	Lakes Entrance	April	Ds	40.5	3	5	29	2	1	3	1:4.4	406 (6)	438 (7)
491	Queenscliff	February	Tn	75.0	1	33	0	0	0	0	–	416 (2)	–
497	Ulladulla	February	Tn	210.5	0	2	3	0	9	0	1:6	429 (17)	491 (16)
540	Ulladulla	March	Tn	164.0	0	1	1	23	3	0	1:27	433 (0)	506 (5)

tiburón, formando los juveniles, machos adultos y hembras adultas grupos diferentes (Springer 1967). Machos y hembras pequeñas de *S. megalops* fueron capturados juntos pero no coincidieron con hembras de talla grande. Asimismo, en un lance se capturó un cardumen compuesto exclusivamente por machos maduros y grandes, mientras que en otras ocasiones se capturaron cardúmenes formados sólo de hembras grandes. Graham (2005) observó un patrón similar frente a Nueva Gales del Sur, donde hembras y machos se encuentran en diferentes regiones y profundidades. Además, las hembras grandes en su primer año de preñez parecieran separarse de las que se encontraban en su segundo año. Las hembras de *S. acanthias* también presentan segregación por condición reproductiva, ya que éstas permanecen en aguas someras durante su primer año de preñez, posiblemente debido a los requerimientos de agua más cálida para el desarrollo embrionario temprano, y luego migran a aguas más profundas durante su segundo año de gestación (Hanchet 1988). Nuestros resultados, aunque fragmentarios, también indican que las hembras de *S. megalops* en su segundo año reproductivo habitan aguas más profundas que las que están en su primer año de preñez.

Las hembras de *S. megalops* alcanzaron tallas mayores que los machos. Frecuentemente se observa dimorfismo sexual en talla entre tiburones y éste es más común entre especies vivíparas ya que, debido a que el modo reproductivo de las hembras es más energéticamente demandante, existe una fuerte presión de selección para una talla más grande (Sims 2003). Varias especies que presentan dimorfismo sexual en talla también muestran segregación sexual (Sims 2003). En mamíferos que presentan dimorfismo sexual los machos alcanzan una mayor talla y buscan hábitats con mayor disponibilidad de alimento, mientras que las hembras prefieren hábitats que brindan mayor protección contra depredadores (Main *et al.* 1996). El uso de hábitats específicos por machos y hembras ha sido registrado para varias especies de tiburón (e.g., McLaughlin y O'Gower 1971, Sims *et al.* 2001). Hembras del tiburón martillo *Sphyrna lewini* (Griffith y Smith) seleccionan hábitats con mayor abundancia de presas de alto contenido energético (Klimley 1987). Las hembras grandes de *Squalus megalops* tuvieron una dieta diferente y consumieron mayor cantidad de presas ricas en energía que los machos y las hembras pequeñas durante el verano y otoño (Braccini *et al.* 2005). Si las hembras de talla grande tienen diferentes requerimientos energéticos, la selección de una calidad de dieta diferente puede resultar en la segregación por talla y sexo (Main *et al*. 1996). Las hembras grandes pueden habitar zonas con mayor disponibilidad de alimento, mientras que los machos y hembras pequeñas cambian preferencias de alimento por áreas con menos depredadores (Bowyer 2004). Otras hipótesis, sin embargo, tales como la migración, diferencias en la capacidad natatoria, evitar a los machos o la agresión entre individuos del mismo tamaño, también han sido propuestas para explicar la segregación entre tiburones (Springer 1967, Sims 2003). En vista de que *S. megalops* es la especie de tiburón de mayor captura incidental en el sureste de Australia (Walker *et al.* 2005), se requiere

is more common among viviparous species, since for females, due to their more energetically demanding reproductive mode, there is a strong selection pressure for a larger body size (Sims 2003). Many species that have sexual size dimorphism also exhibit sexual segregation (Sims 2003). In sexually dimorphic mammals, males attain a larger size and seek habitats with higher food availability, whereas females prefer habitats safe from predation (Main *et al*. 1996). Sex-specific habitat use has been reported for several shark species (e.g., McLaughlin and O'Gower 1971, Sims *et al*. 2001). Female scalloped hammerhead sharks, *Sphyrna lewini* (Griffith and Smith), select habitats with more abundant, energy-rich prey (Klimley 1987). Large female *Squalus megalops* had a different diet and consumed more energy-rich prey than males and small females during summer and autumn (Braccini *et al*. 2005). If large females have different energetic requirements, selection of different diet quality may lead to sexual size segregation (Main *et al.* 1996). Large females may inhabit areas with higher food availability, while males and small females trade off food preference for areas with fewer predators (Bowyer 2004). Other hypotheses, however, such as migration, differences in swimming capabilities, male-avoidance or absence of aggression between similar-sized individuals, have also been proposed to explain segregation among sharks (Springer 1967, Sims 2003). As *S. megalops* is the most common by-catch shark species in southeastern Australia (Walker *et al*. 2005), further information is needed on the location of parturition areas, and on the spatial distribution of juveniles and mature males and females in different breeding condition. A more rigorous sampling design would allow determining the extent of the segregation pattern of *S. megalops* and testing the hypotheses proposed to explain this phenomenon.

Small *S. megalops* were not collected by the sampling gears. The small length-classes are often missing in dogfish studies (Clarke 2000). Gillnets select larger-sized specimens, but demersal trawl nets are likely to catch the smaller *S. megalops*; it has been shown that, when present, the small size-classes are retained by the 90-mm mesh-size codend (Graham 2005). Consequently, small individuals probably occur outside the trawling grounds. For *S. acanthias*, parturition and early life-stages have been reported to be in mid-water (Ketchen 1986), and a pelagic phase has been proposed for juvenile *S. megalops* (Compagno *et al.* 1991). This life strategy would decrease predation risk as larger predatory sharks and teleosts probably occur more frequently near the seabed (Graham 2005).

The sex ratio suggests that either females are more common in the population, or that they are more vulnerable to fishing than males. If the latter, this must be considered in the management of this species, since the selective removal of females may have a disproportionate effect on the reproductive output of the population. The segregation pattern of *S. megalops* also needs to be considered in management plans. Different management of males and females has already been información adicional sobre la localización de las zonas de alumbramiento y sobre la distribución espacial de los juveniles, así como de los machos y las hembras maduras en diferentes condiciones reproductivas. Un diseño de muestreo más riguroso permitiría determinar el grado del patrón de segregación de *S. megalops* y comprobar la hipótesis propuesta para explicar este fenómeno.

No se obtuvieron especímenes pequeños de *S. megalops* con las artes de pesca utilizadas. Las clases de talla pequeña frecuentemente están ausentes en los estudios sobre galludos (Clarke 2000). Las redes de enmalle seleccionan especímenes de mayor tamaño, pero las de arrastre de fondo pudieron capturar *S. megalops* más pequeños. Se ha demostrado que, cuando están presentes, las clases de menor talla son capturadas por el copo de 90 mm de luz de malla (Graham 2005); por tanto, es probable que existan individuos pequeños fuera de las zonas de arrastre. Para *S. acanthias* se ha informado que el alumbramiento y los estadios de vida tempranos se desarrollan en el nivel medio del agua (Ketchen 1986), y para juveniles de *S. megalops* se ha propuesto una fase pelágica (Compagno *et al.* 1991). Esta estrategia de vida podría disminuir el riesgo de predación, ya que los tiburones y teleósteos predadores de mayor talla tienden a encontrarse cerca del fondo del mar (Graham 2005).

La razón de sexos sugiere ya sea que las hembras son más comunes en la población o que son más vulnerables a la pesca que los machos. En este último caso, esto tendría que considerarse en el manejo de la especie puesto que la captura selectiva de hembras pudiera tener un efecto desproporcionado sobre el rendimiento reproductivo de la población. También es necesario considerar el patrón de segregación de *S. megalops* en los planes de manejo. Ya se ha propuesto un manejo diferente de machos y hembras para mamíferos que presentan segregación sexual (Bowyer 2004).

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proposed for mammals showing sexual segregation (Bowyer 2004).

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Determining reproductive parameters for population assessments of chondrichthyan species with asynchronous ovulation and parturition: piked spurdog (*Squalus megalops*) as a case study

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Abstract. Population assessments of chondrichthyan species require several key parameters of their reproductive biology, which were estimated for *Squalus megalops* (Macleay, 1881). Length-at-maturity differed depending on the criterion adopted for defining maturity. In the case of males, length-at-maturity was smallest when condition of seminal vesicles was adopted as a maturity criterion. For females, length-at-maturity was smallest when the largest follicle diameter >3 mm was adopted as the criterion for maturity; this was appropriate only as an indicator of the onset of maturity. Mature males are capable of mating throughout the year. Females have a continuous asynchronous reproductive cycle. The sex ratio of embryos is 1 : 1 and litter size and near-term embryo length increase with maternal length. Females have an ovarian cycle and gestation period of two years. This was reflected in the differences found between the maturity and maternity ogives. Although all females are mature at 600 mm, only 50% of them contribute to annual recruitment each year. Hence, for chondrichthyan species with reproductive cycles of two, three or more years, if maturity ogives are used in population assessments instead of maternity ogives, the models will overestimate recruitment rates.

Extra keywords: asynchrony, Australia, reproduction.

Introduction

Depleted stocks of many teleost and invertebrate species have high potential for recovery but this is generally not the case for many species of chondrichthyes (sharks, rays and chimaeras). Chondrichthyans have several biological characteristics that make them susceptible to fishing overexploitation. Chondrichthyans are mostly long-lived predators that have few offspring, producing close stock–recruitment relationships and slow stock recovery when overfished (FAO 2000). Chondrichthyan populations tend to have lower reproductive rates and lower natural mortality rates, and hence lower biological productivity, than teleost and invertebrate populations. Consequently, only a small proportion of chondrichthyan populations can be removed annually if catches and populations are to remain sustainable (Walker 1998). Fisheries targeting chondrichthyan species have been assessed by population models designed for teleosts, often resulting in inappropriate techniques being applied to these animals (Musick *et al.* 2000; Walker 2004). Assessment of chondrichthyan populations is limited by a lack of biological information (Cortés 1998), especially for non-targeted-species.

Information on the reproductive biology of chondrichthyans is crucial for quantitative analysis of their populations. Measures of the biological productivity of chondrichthyan species, derived from reproductive and natural mortality rates, are required for stock assessments, demographic assessments and ecological risk assessments (Walker 2004). Furthermore, these measures are required in species assessments by wildlife conservation organisations such as the International Union for Conservation of Nature and Natural Resources (IUCN) (Hilton-Taylor 2000). All these assessments use the same information for representing key parameters of reproduction: sex ratio at birth, the relationship between the number of offspring and maternal age or size of animals (litter size) and, sometimes useful for fisheries assessments, the relationship between the proportion of animals in mature condition at any time and the age or size of animals (maturity ogive). Essential for all types of assessment is the relationship between the proportion of the female population contributing to annual recruitment (i.e. females in maternal condition) and the age or size of animals (maternity ogive) (Walker 2005).

Maternal condition is not usually considered or it is incorrectly equated to mature or pregnant conditions in most demographic studies. Maternity ogives of chondrichthyan species populations can be markedly different from maturity ogives

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and pregnancy ogives. For example, off southern Australia, the parturition frequency of school shark (*Galeorhinus galeus*) is triennial so at most one-third of the mature female population contributes to recruitment at the beginning of the following year. Also, length-at-maternity is much larger than length-at-maturity for this species (Walker 2005). Hence, although all females attain maturity at ~1600 mm total length, about one-third of them are in maternal condition in any year. Thus, for chondrichthyan species with complex breeding cycles exceeding one year of duration, if maternity ogives are ignored and only maturity curves are considered in the analysis, population models would overestimate recruitment rates and bias assessments.

Methods for appropriate determination of maternity parameters needed for population assessments of chondrichthyans have only been established for viviparous species with synchronous reproductive cycles (Walker 2005). Although most viviparous chondrichthyans have synchronous mating, gestation and parturition (Hamlett and Koob 1999), in some species with complex breeding cycles, mating, gestation and parturition are asynchronous (Yano and Tanaka 1988; Yano 1993, 1995). For these species, a different approach is required for determining the parameters of maternity ogives for population assessments.

Complex asynchronous breeding cycles of several years duration have been reported for several squalid sharks (Squalidae) (Yano and Tanaka 1988; Yano 1995; Watson and Smale 1998). The piked spurdog (*Squalus megalops* (Macleay, 1881)) provides for a case study of the reproductive information needed for quantitative population studies because this species may have a long and complex ovarian cycle and gestation period (Watson and Smale 1998; Graham 2005). Hence, this shark may have different patterns of maturity condition and maternity condition. Furthermore, *S. megalops* has a high natural abundance in southern Australia (Bulman *et al.* 2001; Graham *et al.* 2001) and, although this shark is among the most caught bycatch species (Walker *et al.* 2005), its abundance has remained stable off New South Wales since it was first surveyed (Graham *et al.* 2001).

The present paper is part of a broad-scale programme for rapid assessment of ecological risk from the effects of fishing on the population status of *S. megalops* and other chondrichthyan species impacted by fishing in southern Australian fisheries. The specific objectives of the present study were to: (*i*) describe the reproductive biology of this species with emphasis on the information needed for quantitative population studies; (*ii*) analyse temporal variation in reproductive condition of mature males; (*iii*) determine sex ratio of embryos; (*iv*) evaluate litter and offspring size–maternal length relationships; (*v*) determine the periodicity of the ovarian cycle and gestation period of females; (*vi*) determine the maturity ogive as a function of length for each sex; and (*vii*) determine pregnancy and maternity ogives as a function of female length.

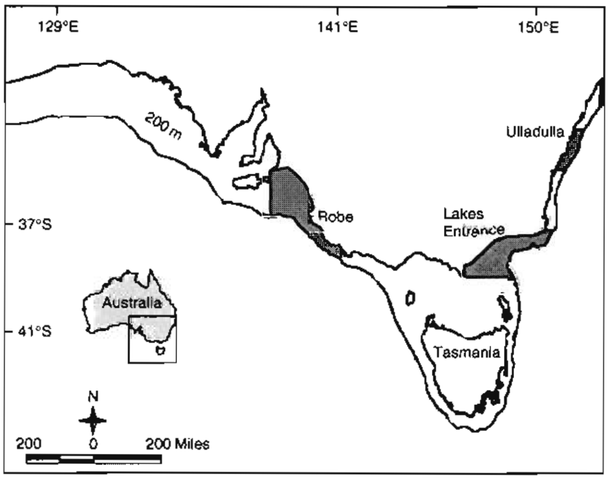

Fig. 1. Map of sampling area showing the three regions compared (shaded) and ports.

Materials and methods

Sampling

Specimens of *Squalus megalops* were obtained from the bycatch of the Australian southern and eastern scalefish and shark fishery in waters off Robe (SA), Lakes Entrance (VIC) and Ulladulla (NSW), Australia (Fig. 1). Samples from Lakes Entrance and Ulladulla were caught by commercial bottom trawl fishing vessels whereas samples from Robe were caught by commercial shark fishing vessels using gill-nets of 6 1/2-inch (165 mm) mesh size. Samples were collected monthly between October 2002 and April 2004, with the exception of August to September, when *S. megalops* seemed to move off the fishing grounds and weather conditions hampered sampling operations. The specimens were sexed, measured (total length, TL, ± 1 mm), weighed (body mass, TM) on an electronic balance (± 1 g), and dissected to investigate their reproductive biology. Mass of liver (LM), gonads (GM) and seminal fluid in seminal vesicles (SFM) were also weighed (± 0.1 g).

Analyses of males

For males, different criteria were used to investigate maturity condition. Length of the left clasper (CL) was recorded from the join in skin near the anus to the distal end (± 1 mm). Macroscopic inspection of condition of clasper calcification (CI), testes (GI), seminal vesicles (VI), seminal fluid (VC) and vas deferens (VD) was undertaken to investigate further maturity by adopting four indices of maturity condition (using Walker's scale, modified for this species, Walker 2005) (Table 1).

Temporal variation in reproductive condition of mature males was investigated by recording the seminal vesicle fullness (VF) using a quarterly scale (0, empty to 4, full) and seminal fluid colouration and consistency (VC: 1, clear to 3, cloudy and thick). For each season, the gonadosomatic index ($GSI = 100\,GM\,TM^{-1}$), the hepatosomatic index ($HSI = 100\,LM\,TM^{-1}$) and the spermatosomatic index ($SSI = 100\,SFM\,TM^{-1}$) for males with VI = 2 were also calculated. Data were not analysed by month owing to small sample sizes for some months. Winter samples of mature males were not considered owing to small sample size ($n = 2$). Temporal variation in HSI, GSI and SSI was tested by ANOVA.

Reproductive cycle of females

For females, macroscopic inspection of condition of ovaries, oviducal glands and uteri was undertaken to investigate sex ratio of embryos,

Table 1. Indices used for staging reproductive condition. Maturity conditions corresponding to each index are also listed (modified from Walker 2005)

Organ	Index	Description	Maturity
Male			
Clasper	CI = 0	Pliable with no calcification and without hooks	Immature
	CI = 1	Partly calcified with small hooks	Immature
	CI = 2	Rigid and fully calcified with evident hooks	Mature
Testis	GI = 1	Undifferentiated thin tissue strip	Immature
	GI = 2	Thickened tissue strip becoming lobular	Immature
	GI = 3	Enlarged with evident testicular lobules	Mature
Seminal vesicles	VI = 1	Thin translucent walls and seminal fluids absent	Immature
	VI = 2	Thickened opaque walls and seminal fluids present	Mature
	VI = 3	Thickened opaque walls and seminal fluids absent	Mature
Vas deferens	VD = 1	Thin line along dorsal surface of abdominal cavity	Immature
	VD = 2	Thickened line that begins to coil	Immature
	VD = 3	Enlarged and fully coiled	Mature
Female			
Ovary	GI = 1	Largest follicles hyaline and of diameter <3 mm	Immature
	GI = 2	Largest follicles white and of diameter 3–14 mm	Immature
	GI = 3	Largest follicles yellow with yolk and of diameter ≥15 mm	Mature
Oviducal gland	OI = 1	Indistinct from anterior uterus	Immature
	OI = 2	Distinct but only partly formed	Immature
	OI = 3	Enlarged and kidney-shaped	Mature
Uterus	UI = 1	Uniformly thin tubular structure	Immature
	UI = 2	Thin tubular structure partly enlarged posteriorly	Immature
	UI = 3	Enlarged tubular structure partly narrow anteriorly	Uncertain
	UI = 4	*In utero* eggs present without macroscopically visible embryos present	Mature
	UI = 5	*In utero* embryos macroscopically visible	Mature
	UI = 6	Enlarged tubular structure distended (post partum)	Mature

Clasper index (CI), gonad index (GI), seminal vesicle index (VI), vas deferens index (VD), oviducal gland index (OI), uterus index (UI).

litter size, growth of embryos, periodicity of the ovarian cycle and gestation period, and mature, pregnant and maternal conditions. Indices were adopted for recording the condition of ovaries (GI), oviducal glands (OI) and uteri (UI) (using Walker's scale, modified for this species, Walker 2005) (Table 1). Maximum width of the left uterus was measured (± 1 mm) to investigate the dynamics of the reproductive cycle. For pregnant females, number of *in utero* eggs or embryos and the sex, uterus (left or right), stage of development (*in utero* egg only, embryo with external yolk or embryo only), and total length (TLE, ± 1 mm) of each embryo were recorded.

Sex ratio of embryos

χ^2 tests with Yates' continuity correction were applied to pregnant females (UI = 4 and 5) to test two hypotheses: (*i*) the number of *in utero* eggs and embryos in the left uterus equalled the number in the right uterus; and (*ii*) the sex ratio of *in utero* embryos was 1 : 1.

Litter and offspring size–maternal length

The relationship between the number of *in utero* eggs or embryos (litter size) and maternal TL, and the relationship between total length of near-term embryos (TLE) (offspring size) and maternal TL were represented by a linear regression model (Walker 2005). Embryos were considered near-term when the external yolk sac was completely absorbed. Females were collected from different regions (Fig. 1) and may exhibit geographical variation in their reproductive parameters (Wourms 1977). ANCOVA was used to test for the effects of region on the linear relationships between maternal TL and litter and offspring size.

Ovarian cycle

To determine the ovarian cycle, the diameter of the 20 largest follicles in each ovary was measured (± 1 mm) to obtain the largest follicle diameter (LFD) for females caught throughout the year. Because the diameters of the largest follicles varied between individual animals and uterus condition, temporal variation of follicle growth was examined separately for each uterus condition defined in Table 1 (Walker 2005). Owing to the asynchronous nature of the reproductive cycle (see 'Results'), only pregnant females (UI = 4 and 5) were used to estimate the ovarian cycle. Pregnant females were arbitrarily classed in five categories based on the size of the embryo they carried: 0 for females carrying *in utero* eggs corresponding to 0 mm TLE, 1 for females carrying embryos <30 mm TLE, 2 for females carrying embryos 30–99 mm TLE, 3 for females carrying embryos 100–199 mm TLE, and 4 for females carrying embryos ≥200 mm TLE. Based on the assumption that LFD from different year classes have the same growth pattern, pregnant females in class 0 from late 2002, classes 1 and 2 from early 2003, class 3 from late 2003, and class 4 from early 2004 were used in a linear model to determine annual growth rate of follicles (Walker 2005). Data from different regions were pooled and no comparisons among regions were performed because no samples were collected from Robe and Ulladulla during May to November.

Gestation period

Gestation period was determined by plotting the percentage of females in uterus condition UI = 4–6 against month and TLE against Julian day. Based on the assumption that embryos from different year classes have the same growth pattern, TLE from the same subset of data selected for the ovarian cycle analysis was used in a growth model. The Gompertz curve is one of the best models of embryonic fish growth (Ricker 1979); hence, this model was fitted to the data subset, holding L_∞ at 230 mm, the average size at birth. Data from different regions were pooled and no comparisons among regions were conducted because no samples were collected from Robe and Ulladulla during May to November.

Maturity, pregnancy and maternity ogives

Logistic models were used to determine the proportion of mature males and females at any TL and, for females, the proportion in pregnant and maternal conditions (Punt and Walker 1998; Roa *et al.* 1999). Model parameters and the ogives with 95% confidence intervals (CI) were estimated by the method of maximum likelihood of the probit procedure using the SAS statistical package (SAS Institute, Cary, NC, USA) (Walker 2005). Given the uncertainty in determining maturity in males (Conrath 2004), indices for each of four separate methods were used and the results compared. A male was classed as in mature condition if CI = 2, GI = 3, VI = 2–3, or VD = 3; otherwise it was classed as immature. Logistic curves and associated parameters were determined for each maturity criterion. Females had a complex reproductive cycle (see 'Results'); hence, as for males, different maturity criteria were adopted and the results compared. A female was classed as in mature condition if GI = 3, OI = 3, or UI = 4–6; otherwise it was classed as immature. In addition, the effect of adopting three alternative maturity criteria based on LFD was assessed: LFD >3 mm (Walker 2005) (for onset of maturity), LFD ≥15 mm (present study) and LFD ≥20 mm (Yano and Tanaka 1988; Watson and Smale 1998). Logistic curves and associated parameters were determined for each maturity criterion. Regional comparisons of samples from Lakes Entrance and Robe were undertaken using the logistic procedure of the SAS statistical package (SAS Institute, Cary, NC) (Walker 2005). Samples from Ulladulla were not included because all sharks were in mature condition and hence the maturity ogive was not calculated.

For the analysis of pregnant females, a female was classed as in pregnant condition if UI = 4–5; otherwise it was classed as non-pregnant. For the maternity analysis, a female was classed as in maternal condition if, had it survived, it would have given birth by the end of 2003 or early 2004 (i.e. it contributed to annual recruitment at the beginning of 2004). Hence, for each pregnant female, parturition time was calculated using the embryo growth model. Pregnancy and maternity ogives were determined using logistic models. Model parameters and the ogives with 95% CI were estimated by the method of maximum likelihood of the probit procedure using the SAS statistical package (Walker 2005). Given that parturition frequency is biennial (see 'Results'), for SAS probit analysis of maternity condition, the parameter P_{max} (maximum proportion of animals in maternal condition) was altered from 1.0 to 0.5. The SAS output was then multiplied by 0.5 to obtain the parameters of the maternity ogive, with 95% CI (Walker 2005). Assuming that sampling was not biased for pregnant or non-pregnant females, pregnancy and maternity ogives were determined using pooled data from different regions; hence, no regional comparisons were made for these ogives.

Results

Analyses of males

A total of 207 male *Squalus megalops* (274–470 mm TL) were collected for reproductive analyses. Male sharks were mostly sampled from Lakes Entrance (Fig. 1) so no regional comparisons were performed. Clasper length (CL) showed a sigmoidal relationship with TL. Claspers grew gradually in animals <350 mm TL, followed by rapid growth until 385 mm TL and 27 mm CL (CI = 2), which several indicators suggest is the TL for the onset of maturity.

Maturity ogives differed depending on the maturity criterion adopted (Fig. 2*e*). The ogive based on maturity condition of seminal vesicles (VI = 2 or 3) showed a value of TL at which 50% of the population was mature (L_{50}) (with 95% CI) of 373 (368, 377) mm (Fig. 2*a*). This value was considerably smaller than those obtained using other maturity criteria. The ogives based on vas deferens (VD = 3), clasper (CI = 2) and gonad (GI = 3) conditions were in reasonable agreement and provided values of L_{50} of 392 (388, 396), 393 (390, 395) and 398 (395, 401) mm respectively (Figs 2*b*–2*d*).

Irrespective of which maturity index was used, males classed as mature were found throughout the year (Fig. 3). Statistical testing of the frequency of males in different GI, CI, VI and VD conditions was not carried out owing to the opportunistic nature of the sampling design and possible size and sex aggregation of the sharks; however, mature males (GI = 3, CI = 2, VI = 2–3 or VD = 3) were collected from each season (Figs 3*a*–3*d*). The frequency of vesicle fullness (VF) of mature males with VI = 2 was similar throughout the year; most mature males had full seminal vesicles (VF = 4) (Fig. 3*e*) containing cloudy and thick seminal fluids (VC = 3) (Fig. 3*f*). There were no seasonal differences in the maturity condition of mature males. Mature males had similar values of mean HSI throughout the sampling period (ANOVA: $F_{2,117} = 2.19$, $P = 0.1164$). Also, no seasonal variation was found in the mean GSI (ANOVA: $F_{2,114} = 0.94$, $P = 0.3939$) and mean SSI (ANOVA: $F_{2,112} = 1.14$, $P = 0.3241$). It appears that mature males are capable of mating throughout the year.

Reproductive cycle of females

Analyses of 722 female *S. megalops* (270–635 mm TL) suggested that females had a continuous asynchronous reproductive cycle. There was an increase in LFD with uterus width for females ovulating for the first time (UI = 1–3) (Fig. 4*a*). Ovulation occurred once LFD reached ~40 mm and uterus reached a width of ~18 mm. For pregnant females carrying *in utero* eggs (UI = 4) or embryos at an early stage of development (UI = 5_1), LFD was small. The follicles enlarged throughout gestation synchronously with embryonic growth and were ready to be ovulated when embryos were near-term, indicating that fertilisation and the gestation of a subsequent litter can occur immediately after parturition. This was supported by the significant correlation between LFD and TLE ($r = 0.954$; $n = 544$; $P < 0.0001$) (Fig. 4*b*).

Sex ratio of embryos

Macroscopically visible *in utero* eggs and embryos were examined in 308 pregnant females (UI = 4 or 5). Most of these females (72.7%) carried only one egg or embryo per uterus and no female was observed to carry eggs and embryos at the same time. Significant differences were found in the number of *in utero* eggs and embryos between the left uterus and the right uterus ($\chi^2 = 15.882$; d.f. = 1; $P < 0.001$). Of

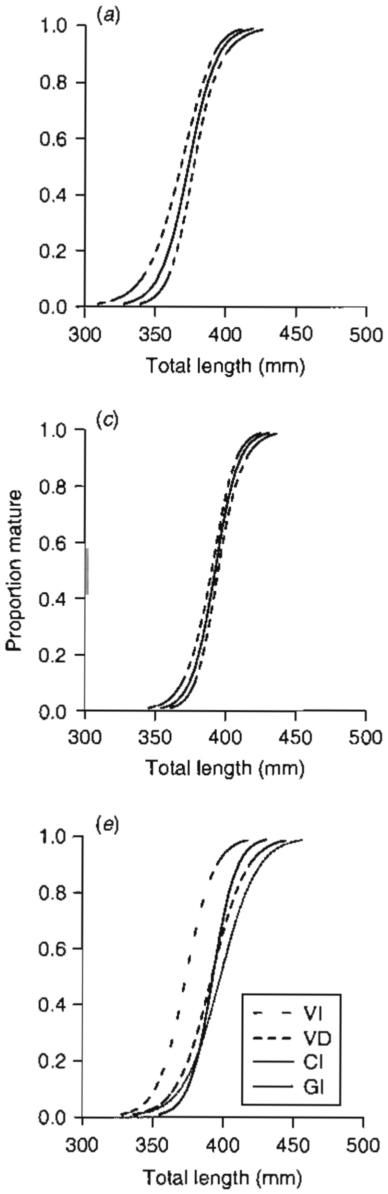

Fig. 2. Male length-at-maturity ogives. Proportion of male population in mature condition *v.* total length with 95% confidence intervals (- - -) determined from (*a*) seminal vesicle condition (VI), (*b*) vas deferens condition (VD), (*c*) clasper condition (CI), (*d*) testis condition (GI), and (*e*) comparison of mean ogives for VI, VD, CI and GI. Values of parameters and statistical quantities for the equation $P = P_{\max}(1 + e^{-\ln(19)((l-l_{50})/(l_{95}-l_{50}))})^{-1}$ used in the probit analysis are in Table 2.

a total of 668 eggs and embryos counted, 386 (57.8%) were present in the right uterus. However, when the analysis was performed on pregnant females carrying up to two *in utero* eggs or embryos, no significant differences were found between the left uterus and right uterus ($\chi^2 = 3.561$; d.f. = 1; $P = 0.059$). A total of 450 embryos was sexed of which 154 (34.2%) were male, 145 (32.2%) were female, and 151 (33.6%) were classed as 'unknown sex' owing to their early stage of development. The sex ratio of embryos was not significantly different from 1 : 1 ($\chi^2 = 0.214$; d.f. = 1; $P = 0.644$).

Litter and offspring size–maternal length

Litter size was recorded for 308 pregnant females. All females carrying only one embryo were excluded from the analysis because it was assumed that they had aborted embryo(s)

Table 2. Values of parameters and statistical quantities for the maturity ogives of males

Maturity criterion	L_{50} (CI)	L_{95} (CI)	P_{max}	n	ML	P
Seminal vesicle condition	373 (368, 377)	403 (399, 409)	1	201	−113.62	***
Vas deferens condition	392 (388, 396)	428 (422, 437)	1	172	−141.71	***
Clasper condition	393 (390, 395)	417 (413, 422)	1	207	−169.12	***
Testis condition	398 (395, 401)	436 (430, 444)	1	207	−246.96	***

l is total length (TL), P is the proportion of animals at TL l, L_{50} and L_{95} are parameters, P_{max} is an asymptotic constant, n is the total number of animals, ML is maximum likelihood, and P is the probability of statistical significance (***$P < 0.001$).

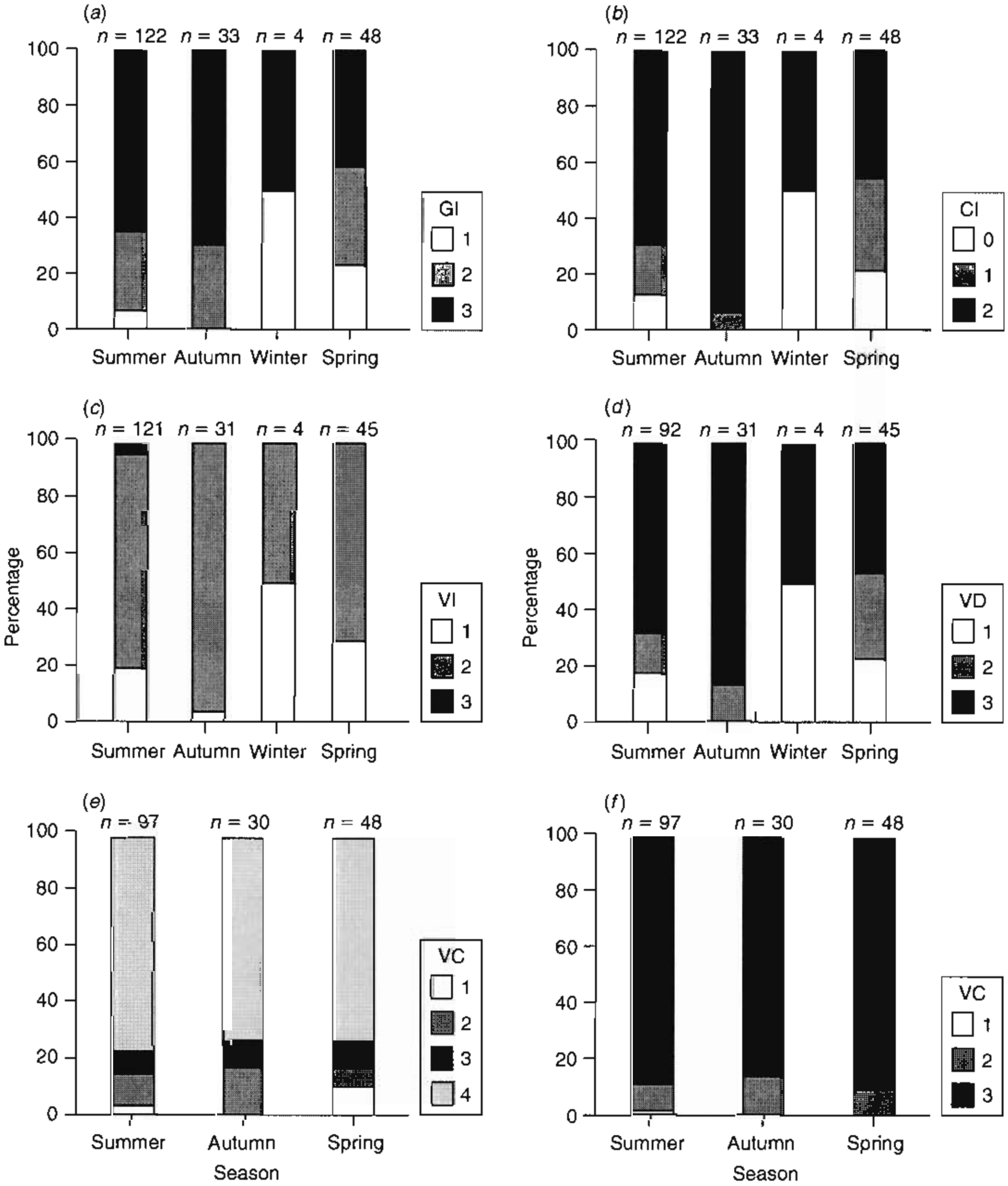

Fig. 3. Percentage of male sharks at different maturity condition collected from different seasons. (*a*) Gonad index (GI); (*b*) clasper index (CI); (*c*) vesicle index (VI); (*d*) vas deferens index (VD); (*e*) vesicle fullness (VF) for males with VI = 2; (*f*) seminal fluid colouration (VC) for males with VI = 2 and VF = 4.

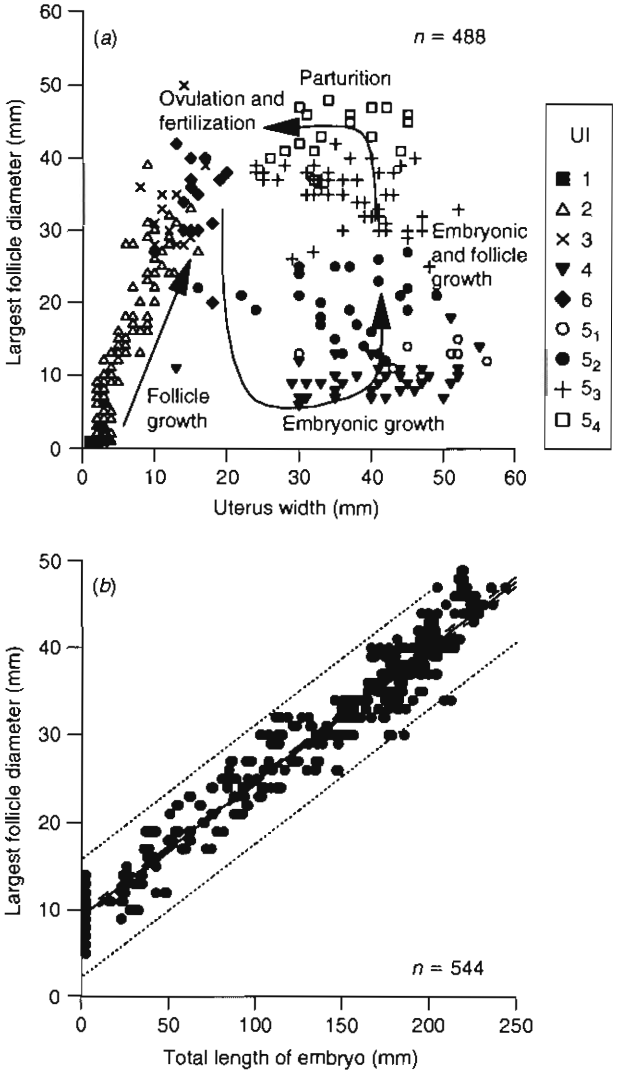

Fig. 4. Relationships between largest follicle diameter (LFD) and (*a*) uterus width for females in different uterus condition (UI) and (*b*) total length of embryo (TLE) with 95% confidence intervals (- - -) and predicted intervals (···) (see Table 1 for UI definition). LFD = 0.153 TLE + 9.303; $r^2 = 0.931$.

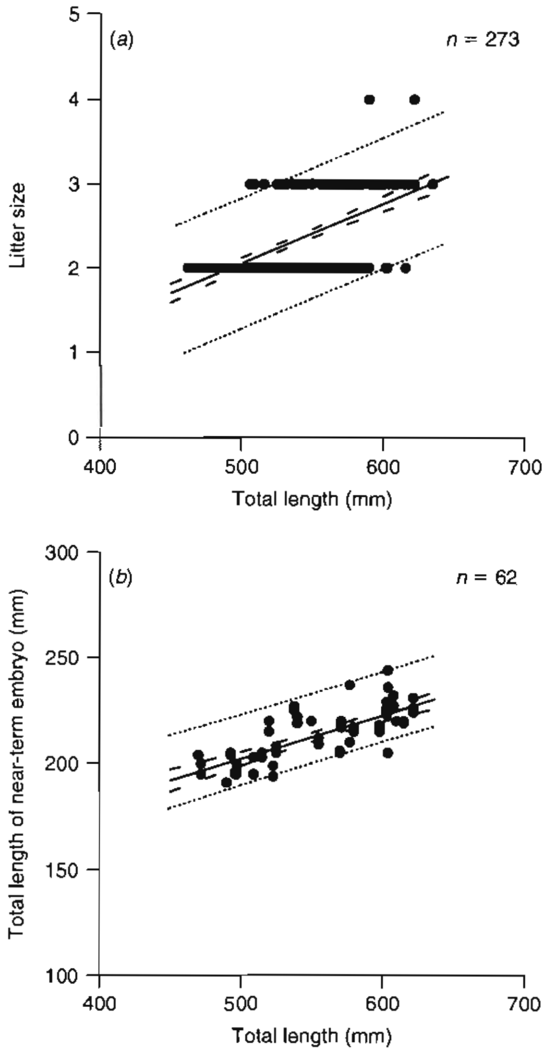

Fig. 5. Relationship between maternal total length (TL) and (*a*) litter size and (*b*) total length of near-term embryos (TLE) with 95% confidence intervals (- - -) and predicted intervals (···). Litter size = 0.00711 TL − 1.503; $r^2 = 0.330$; TLE = 0.203 TL + 100.6; $r^2 = 0.587$.

owing to stress capture. This assumption was supported by the occasional presence of embryos on the deck of the vessels (J. M. Braccini, personal observation) and because these females had empty uteri with stretched and vascularised walls, suggesting the loss of one or more embryos. Uteri containing one or two embryos had turgid walls, indicating that abortion had not occurred. Regional differences detected in the relationship between litter size and maternal TL (ANCOVA: $F_{2,274} = 3.87$, $P = 0.022$) were considered an artefact of the sampling method. Samples from Lakes Entrance and Ulladulla were collected by bottom trawl nets whereas those from Robe were collected by gill-nets of 6 1/2-inch (165 mm) mesh size. For *S. megalops*, 6 1/2-inch gill-nets selected for large-sized females (J. M. Braccini, personal observation) and this is likely to have created apparent regional differences in the litter size–maternal TL relationship caused by sampling bias or length-selective fishing mortality. The results were therefore presented pooling the three regions. Litter size for most females was two (69.3%) or three (30.0%) and only a few of them carried four (0.7%) *in utero* eggs or embryos. Litter size showed a linear relationship with TL ($F_{1,273} = 132.38$, $P < 0.001$) (Fig. 5*a*).

Embryo length (TLE) was recorded for 62 near-term embryos (191–244 mm TLE) and the mean relative length-at-birth (with 95% CI) was 38.5 (35.6, 42.4)% of maternal TL. No regional differences in the relationship between TLE and maternal TL (ANCOVA: $F_{2,60} = 0.67$, $P = 0.515$)

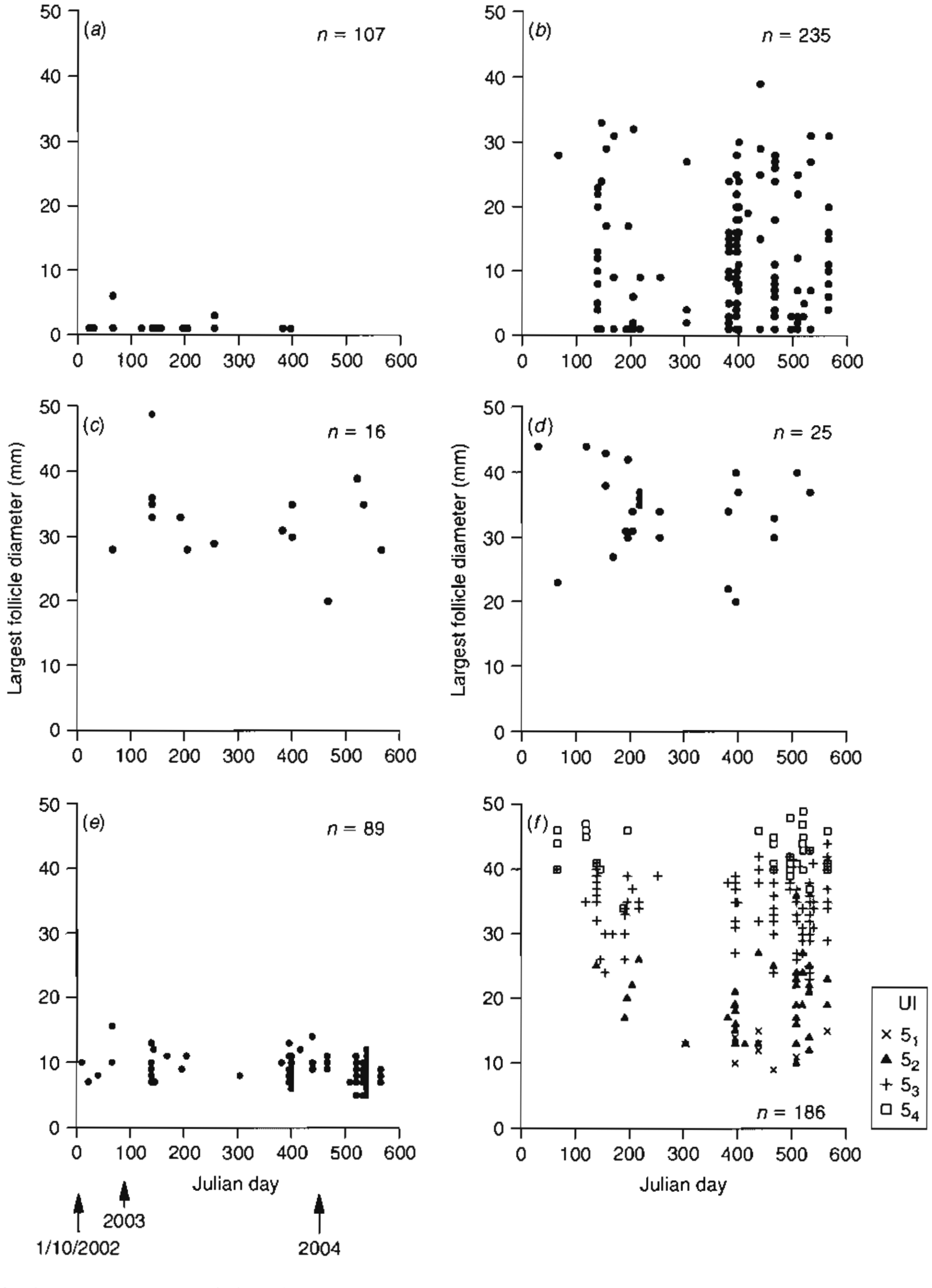

Fig. 6. Ovarian cycle. Relationship between largest follicle diameter and Julian day for (*a*) uterus index (UI) = 1, (*b*) UI = 2, (*c*) UI = 3, (*d*) UI = 6, (*e*) UI = 4 and (*f*) UI = 5.

were detected, so samples collected from different regions were pooled for subsequent analyses. Near-term embryo length increased linearly with maternal TL ($F_{1,60} = 85.40$, $P < 0.001$) (Fig. 5*b*).

Ovarian cycle

Largest follicle diameter (LFD) was recorded for 658 females and ranged from 1 to 49 mm. Females with uterus condition (UI) = 1 always had small follicles (Fig. 6*a*). Females with UI = 2 showed a wide range of LFD (1–39 mm) at any time (Fig. 6*b*), indicating that follicles can approach full size before the uteri were fully developed. Females with UI = 3 or 6 were observed carrying large follicles at all times of the year (Fig. 6*c*,*d*), suggesting that follicle enlargement and ovulation are not temporally synchronous between animals. For animals with UI = 4, LFD was relatively small indicating

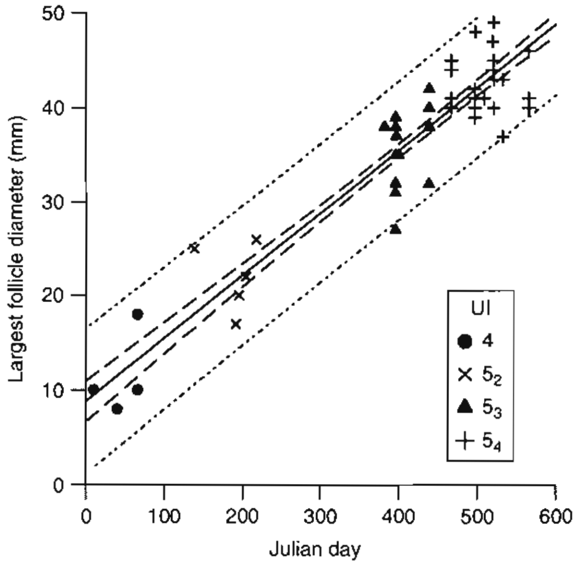

Fig. 7. Hypothetical follicle development curve for females in uterus condition (UI) = 4 and 5. Linear model fitted to selected subset of data with 95% confidence intervals (- - -) and predicted intervals (···). Largest follicle diameter = 0.07 Julian day + 8.797; $r^2 = 0.874$.

that ovulation was complete; no animals were observed in the process of ovulation (Fig. 6*e*). Wide variation of LFD (6–49 mm) was observed for pregnant females carrying embryos (UI = 5) (Fig. 6*f*). Females carrying small embryos had small follicles whereas females carrying near-term embryos had large follicles, suggesting that ovulation immediately follows parturition. Furthermore, only a small percentage of mature females (8.3%) were in UI = 6 condition and they all carried large follicles, indicating a short period between pregnancies. There was a linear relationship between LFD and Julian Day ($F_{1,104} = 709.64$, $P < 0.001$) (Fig. 7), indicating linear follicular growth. Annual growth of LFD was 24 mm y^{-1}, suggesting an ovarian cycle of ~19 months.

Gestation period

A total of 423 embryos was measured and each of 152 *in utero* eggs was assigned a TLE value of 0 mm for determining gestation period. *S. megalops* was an asynchronous breeder in which ovulation, parturition and mating did not occur at any particular time of the year. Females carrying *in utero* eggs (UI = 4) or near-term embryos (UI = 5_4) were observed throughout the year, providing further evidence of no pattern of temporal periodicity in the reproductive cycle (Figs 8*a*, 8*b*). Furthermore, embryos at different stages of development could be found at all times of the year. Based on the Gompertz growth model, annual growth of embryos was 170 mm y^{-1}, suggesting a gestation period of ~2 years (Fig. 8*c*).

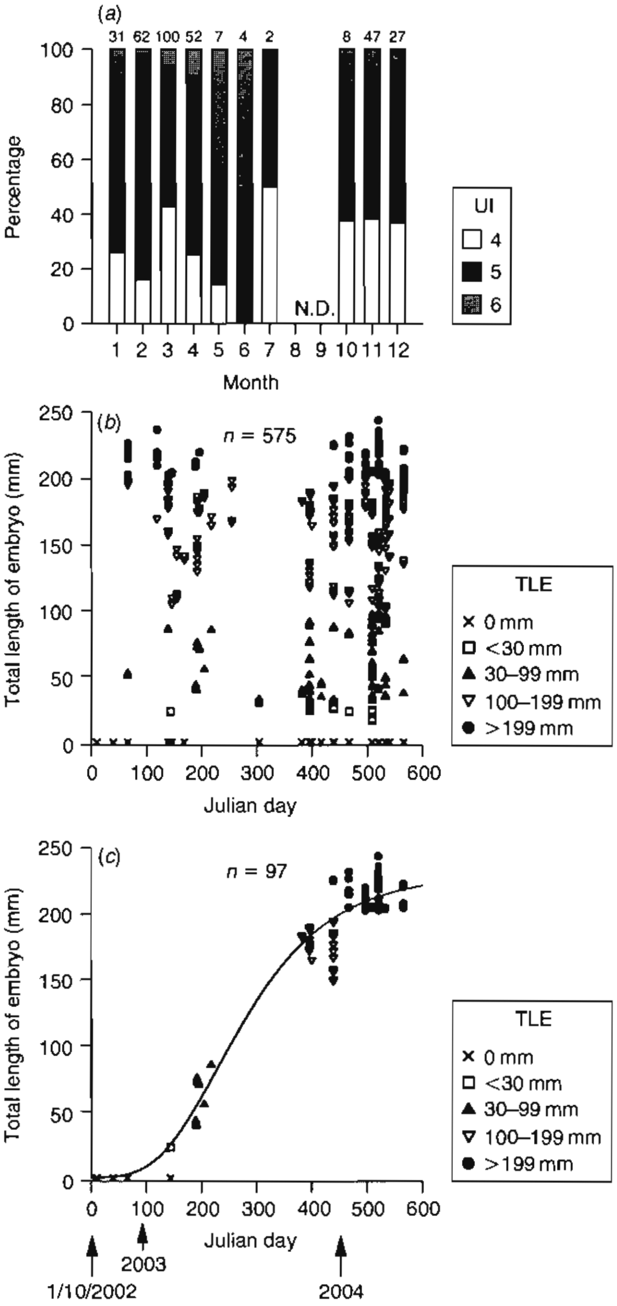

Fig. 8. Gestation period. (*a*) Distribution of different stages of maturity of females in uterus condition (UI) = 4–6 during the year. Sample sizes are shown above bars. (*b*) Length of embryos (TLE) collected during the sampling period. (*c*) Hypothetical growth curve with Gompertz model fitted to the selected subset of data. $TLE = 230e^{(-8.068e^{(-0.009t)})}$; $r^2 = 0.9$. N.D.: no data.

Maturity, pregnancy and maternity ogives

Maturity ogives of females differed depending on the maturity criterion adopted (Fig. 9*g*). When the maturity criterion used was LFD >3 mm (onset of maturity) length at which 50% (L_{50}) of the animals were in mature condition (with 95% CI) was 459 (457, 461) mm (Fig. 9*a*). When LFD ≥15 mm and uteri condition (UI = 4, 5 or 6) were used, L_{50} was 484

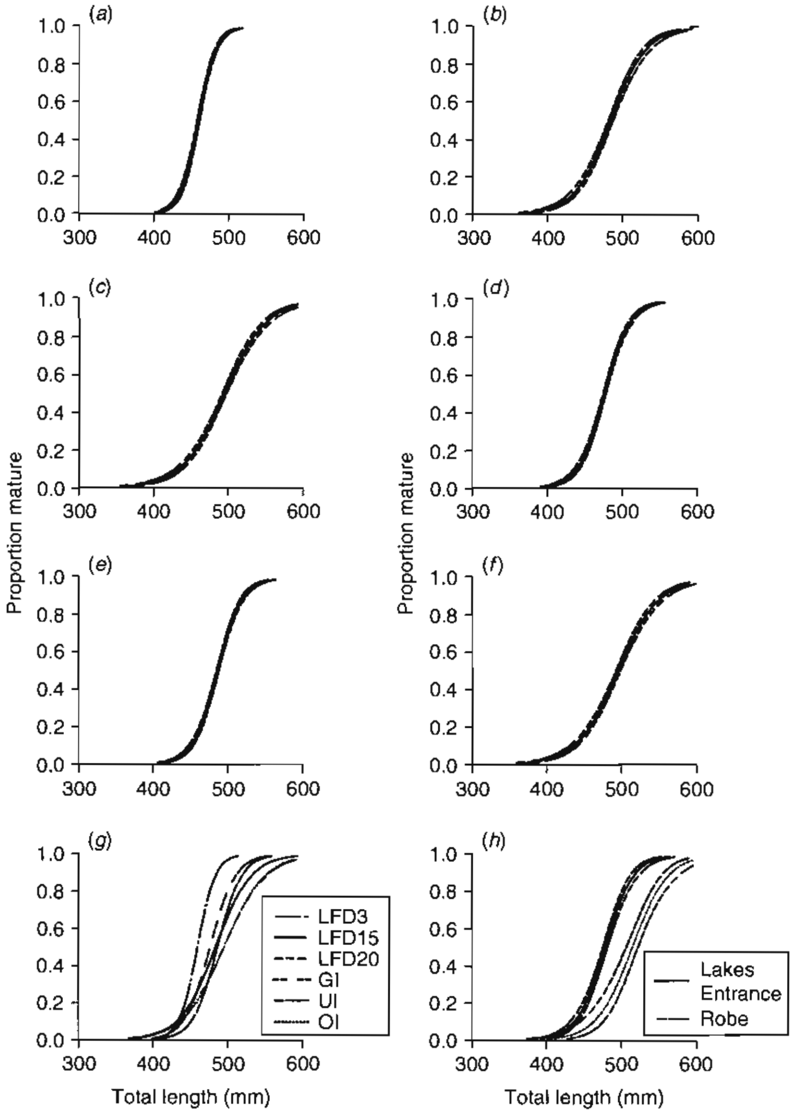

Fig. 9. Female length-at-maturity ogives. Proportion of female population in mature condition against total length with 95% confidence intervals (- - -) determined from (*a*) largest ovarian follicle diameter (LFD) >3 mm (LFD3), (*b*) LFD ≥15 mm (LFD15), (*c*) LFD ≥20 mm (LFD20), (*d*) ovary condition (GI), (*e*) uteri condition (UI), and (*f*) oviducal gland condition (OI). (*g*) Comparison of mean ogives for LFD3, LFD15, LFD20, GI, UI, and OI, and (*h*) comparison between maturity ogives for females from Lakes Entrance and Robe with 95% confidence intervals (- - -) based on the maturity criterion LFD15. Values of parameters and statistical quantities for the equation $P = P_{max}(1 + e^{-\ln(19)((l-l_{50})/(l_{95}-l_{50}))})^{-1}$ used in the probit analysis are in Table 3.

(481, 487) mm and 486 (485, 488) mm respectively (Figs 9*b*, 9*e*). The ogives for LFD ≥20 mm and oviducal gland condition (OI = 3) were similar (Figs 9*c*, 9*f*) and showed a larger value of L_{50} of 495 (492, 498) and 495 (491, 499) mm respectively. Finally, L_{50} based on ovarian condition (GI = 3) was 477 (475, 479) (Fig. 9*d*).

The criterion used to test for the effects of region on the maturity ogives of females was LFD ≥15 mm. This criterion was preferred to other criteria because follicles of 15 mm diameter were yellow, indicating that vitellogenesis was well advanced and because the ogive and the value of L_{50} obtained were in reasonable agreement with most of the

Table 3. Values of parameters and statistical quantities for the maturity ogives of females

Maturity criterion	L_{50} (CI)	L_{95} (CI)	P_{max}	n	ML	P
LFD >3 mm	459 (457, 461)	491 (488, 495)	1	706	−390.86	***
LFD ≥15 mm	484 (481, 487)	554 (547, 563)	1	616	−647.38	***
LFD ≥20 mm	495 (492, 498)	577 (570, 586)	1	615	−1131.75	***
Ovaries condition	477 (475, 479)	527 (522, 531)	1	621	−879.03	***
Uteri condition	486 (485, 488)	534 (530, 538)	1	719	−1231.29	***
Oviducal gland condition	495 (491, 499)	573 (564, 584)	1	584	−563.97	***

l is total length (TL), P is the proportion of animals at TL l, L_{50} and L_{95} are parameters, P_{max} is an asymptotic constant, n is the total number of animals, ML is maximum likelihood, and P is the probability of statistical significance (***$P < 0.001$).

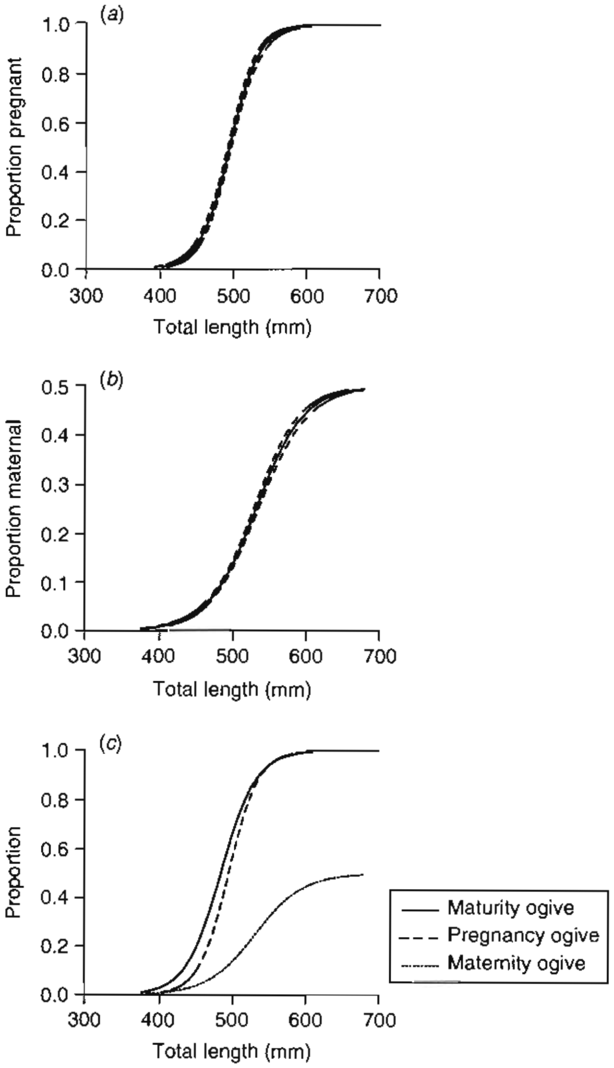

Fig. 10. Female length-at-pregnancy and maternity ogives. Proportion of female population in (*a*) pregnancy and (*b*) maternal conditions against total length with 95% confidence intervals (- - -). (*c*) Comparisons between maturity, pregnancy and maternity ogives. Values of parameters and statistical quantities for the equation $P = P_{max}(1 + e^{-\ln(19)((l-l_{50})/(l_{95}-l_{50}))})^{-1}$ used in the probit analysis are in Table 4.

other criteria considered. Significant differences were found in the maturity ogives of females from Lakes Entrance and Robe ($P < 0.0001$) (Fig. 9*h*). The value of L_{50} for females from Lakes Entrance was 478 (475, 482) mm whereas the value of L_{50} for females from Robe was 514 (506, 523) mm. However, as in the case of the litter size–maternal TL relationship, these could be apparent differences owing to the effects of length-selectivity of the 6 1/2-inch gill-net used in Robe. Such length selectivity might distort the maturity ogive by the effects of sampling bias and length-selective fishing mortality.

Length at which 50% of the female population was pregnant was 495 (492, 497) mm (Fig. 10*a*); however, at any length, at most 50% of the female population was in maternal condition (Fig. 10*b*). The TL-at-maternity and TL-at-pregnancy were larger than TL-at-maturity (Fig. 10*c*). Although all females were mature at 600 mm, only half of the population was in maternal condition and hence contributing to annual recruitment.

Discussion

Analyses of males

Given uncertainty as to the best descriptor of maturity of male sharks (Conrath 2004), the results for four indices were compared in the present study. When condition of seminal vesicles was used, L_{50} was considerably smaller than when conditions of gonads, vas deferens or clasper calcification were used. Walker (2005) also found a smaller value of L_{50} when comparing the condition of seminal vesicles with gonad condition or clasper calcification in *Galeorhinus galeus*. These findings suggest that seminal vesicle condition might class some males as mature even though they may not be capable of mating as, for example, they may not have fully functional claspers. Watson and Smale (1998) and Graham (2005) found similar values of L_{50} to those obtained in the present study based on conditions of the gonads, vas deferens and clasper calcification. For male *Squalus megalops*, these criteria for maturity condition gave similar values of L_{50} and similar maturity ogives, suggesting that any of these criteria could be used to determine maturity.

Table 4. Values of parameters and statistical quantities for the pregnancy and maternity ogives

Condition	L_{50} (CI)	L_{95} (CI)	P_{max}	n	ML	P
Pregnant	495 (492, 497)	554 (548, 560)	1	720	−777.19	***
Maternal	531 (528, 534)	626 (618, 635)	0.5	522	−1983.39	***

l is total length (TL), P is the proportion of animals at TL l, L_{50} and L_{95} are parameters, P_{max} is an asymptotic constant, n is the total number of animals, ML is maximum likelihood, and P is the probability of statistical significance (***$P < 0.001$).

Irrespective of maturity criterion, mature males were observed in all seasons and none of GSI, HSI and SSI exhibited seasonal variation, indicating that males are in mating condition throughout the year. A similar pattern is reported for male *S. megalops* from South Africa (Watson and Smale 1998) and several other shark species (Parsons and Grier 1992). This would be advantageous for species that inhabit environments with little variation in environmental cues (e.g. deep sea and tropics) or where mate location may be difficult (e.g. deep sea and open ocean) or both (Wourms 1977; Parsons and Grier 1992). *S. megalops* inhabits waters of the continental shelf and upper continental slope to 510 m (Last and Stevens 1994) so it cannot be considered a deepwater shark. However, most squalid species occur in deeper waters on the continental slope (Last and Stevens 1994); hence, the apparent lack of seasonality in the reproductive cycle of male *S. megalops* may be an ancestral trait.

Reproductive cycle of females

Females have a continuous reproductive cycle. Following ovulation, follicles begin to undergo vitellogenesis again concurrently with embryonic growth and are ready for ovulation and fertilisation immediately after parturition. A similar pattern is reported for *S. megalops* from New South Wales, Australia (Graham 2005) and South Africa (Watson and Smale 1998) and for other species of *Squalus* (Kibesaki 1954; Jones and Geen 1977; Chen *et al.* 1981) although some female spiny dogfish (*Squalus acanthias*) have a resting period between pregnancies (Jones and Geen 1977; Hanchet 1988). The few observed mature female *S. megalops* in the present study that were not pregnant all carried enlarged follicles ready for ovulation, suggesting a very short period between pregnancies.

Sex ratio of embryos

The sex ratio of embryos is 1 : 1. A 1 : 1 embryo sex ratio is also reported for *S. megalops* from South Africa (Watson and Smale 1998) and for other squalid species (Hanchet 1988; Yano 1995). A 1 : 1 embryo sex ratio is expected for a sexually balanced population, assuming that males and females have similar mortalities. Less straightforward is, however, the distribution of embryos between uteri. When all pregnant females were considered in the analysis, a larger proportion carried eggs or embryos in the right uterus than in the left uterus, but analysis of females carrying up to two eggs or embryos showed that eggs or embryos were carried in similar numbers between the two uteri. Space in the body cavity of viviparous sharks is important during embryonic development (Bass 1973), particularly for species carrying relatively large-sized embryos, like *S. megalops*. In this shark, the stomach is positioned on the left side of the body cavity; thus, when carrying more than two embryos, space would be maximised if females hold more embryos in the right uterus.

Litter and offspring size–maternal length

The litter size and embryo length of *S. megalops* increased with maternal TL. The pattern of increasing number of embryos (Hanchet 1988; Yano and Tanaka 1988; Taniuchi *et al.* 1993) and length of near-term embryos (Hanchet 1988; Guallart and Vicent 2001) with maternal TL is reported for other squalid species. This pattern is also observed in *S. megalops* from South Africa and it may be related to an increase in space in the body cavity (Watson and Smale 1998).

Ovarian cycle and gestation period

Ovulation and parturition in *S. megalops* exhibit no pattern of temporal periodicity, suggesting that this shark is an asynchronous breeder. Most viviparous chondrichthyans have synchronous mating (Hamlett and Koob 1999), although in a few species mating is asynchronous (Yano and Tanaka 1988; Yano 1993, 1995). For chondrichthyans with synchronous mating, the largest follicle diameter (LFD) and the size of the embryos are recorded through time to determine the ovarian cycle and gestation period. However, this method cannot be applied for species with asynchronous mating given that follicles or embryos at very different stages of development are found at all times of the year. The ovarian cycle of three deepwater squalid species could not be determined using this method (Yano and Tanaka 1988). Watson and Smale (1998) used a similar approach to estimate the gestation period of *S. megalops* without any success. In the present study, ovarian cycle and gestation period were determined using the linear and Gompertz growth models, respectively, on a subset of data from different years. These models gave a good fit to the data and allowed an approximate determination of the ovarian cycle and gestation period. For other shark species, the linear (Walker 2005) and Gompertz (Hanchet 1988) models have been used successfully for determining periodicity of ovarian cycle and gestation period respectively.

Squalus megalops has an ovarian cycle and gestation period of ~2 years. Periodicity of ovarian cycle and gestation are crucial for defining maternal condition of female chondrichthyans; they need to be determined for population assessments of chondrichthyan species. Most viviparous sharks have gestation periods of about one year (Stevens and McLoughlin 1991; Hamlett and Koob 1999). However, for species producing large-sized follicles, such as most squalid species (Chen *et al.* 1981; Hanchet 1988; Guallart and Vicent 2001), ovarian cycle and gestation period are two, three or more years. Given that ovarian cycle and gestation period in *S. megalops* are biennial and that development of follicles and embryos occurs concurrently, it is expected that parturition frequency for the population is also biennial.

Maturity, pregnancy and maternity ogives

The different criteria used to calculate the maturity ogive of females are in reasonable agreement in most cases. The condition of the reproductive tract and ovaries has been commonly recorded to determine maturity of female chondrichthyans (Jones and Geen 1977; Hanchet 1988; Watson and Smale 1998) though Walker (2005) proposed measuring the diameter of the largest follicle (LFD) as an objective criterion of maturity condition least prone to observer bias. To determine the onset of maturity of *G. galeus*, he classed females as having reached the onset of maturity if LFD was >3 mm. In the present study, the smallest value of L_{50} was obtained using this criterion. For *S. megalops*, follicles <15 mm diameter were white, whereas follicles >15 mm were yellow, indicating that vitellogenesis began at about this size. Furthermore, the ogive and the value of L_{50} obtained using the criterion LFD ≥15 mm were in reasonable agreement with most of the other criteria considered, suggesting that vitellogenesis starts when other reproductive structures begin development. Thus, LFD ≥15 mm criterion was adopted for regional comparisons.

Differences in the maturity ogive of females from Lakes Entrance and Robe were found. Spatial differences in size-at-maturity could occur when different age or size classes from different locations are sampled or from length-selective fishing mortality (Walker 2005). In the present study, regional differences in size-at-maturity could be a result of length-selectivity of the 6 1/2-inch gill-net used off Robe, selecting for the largest females and possibly distorting the maturity ogive. Graham (2005) reported similar values of length-at-maturity for females collected from New South Wales. In South Africa, female *S. megalops* also showed a similar length-at-maturity (Watson and Smale 1998) despite collecting a larger range of sizes (the largest female being 782 mm TL). This suggests that females from New South Wales, South Africa and south-eastern Australia would have similar maturity parameters. Taniuchi *et al.* (1993) reported spatial variation in the length-at-maturity of female shortspine spurdogs (*Squalus mitsukurii*) from four different locations off Japan and attributed it to differences in local environmental conditions. However, they collected a different range of sizes from each location and their samples from each location were obtained from different depths and years. Given that females of squalid species can be segregated by stage of maturity and size (Yano and Tanaka 1988), the geographical differences reported by these authors may be apparent and another example of how using females of different size classes can distort maturity ogives.

The length at which 50% of the female population was pregnant was slightly larger than the length at which 50% was mature. This suggests that once females attain maturity most of them become pregnant soon after first ovulation and parturition thereafter. These findings further support the hypothesis of a continuous breeding cycle. However, for population assessment models, it is important to distinguish the mature condition from pregnant and maternal conditions. For species with reproductive cycles of several years duration, a more critical relationship is the proportion of females in maternal condition.

Only half of the pregnant female population is in maternal condition in any year and contributes to annual recruitment. The size of a population depends on the rates of birth, death and migration. For viviparous chondrichthyans, birth rate can be calculated from the number of females in the population, its fecundity rate and the proportion of females contributing to annual recruitment (Walker 2005). Thus, for chondrichthyan species with one year continuous reproductive cycles, calculation of population size can be performed using maturity or maternity ogives as all mature females contribute to annual recruitment each year. However, for species with a reproductive cycle of more than one year, such as *S. megalops*, population size would differ depending on which ogive is used.

In conclusion, determining maternity ogives from information on the timing of ovulation, period of gestation and parturition frequency is more complex for asynchronous species than, as shown by Walker (2005), for synchronous species. Most squalid species are deepwater asynchronous breeders with reproductive cycles of several years duration. Also, many species are endemic and have restricted distributions. Given these biological and ecological attributes, they are particularly vulnerable to fishing overexploitation. Consequently, their populations require special management and a different approach to determine reproductive parameters for population assessments. Reproductive parameters of *S. megalops* were determined, despite this shark having an asynchronous reproductive cycle. Mature males and females are capable of mating throughout the year and females have a two-year continuous cycle. Thus, although all females are mature at 555 mm TL, only 50% of them are in maternal condition, contributing to annual recruitment each year. Hence, for chondrichthyan species with reproductive cycles of two, three or more years, if maturity ogives are used in population assessments instead of maternity ogives, models will overestimate recruitment rates.

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RESEARCH ARTICLE

Embryo development and maternal–embryo nutritional relationships of piked spurdog (*Squalus megalops*)

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Abstract The maternal–embryo relationship was determined for the piked spurdog (*Squalus megalops*). In addition, the increase in offspring size with maternal size was studied and the embryonic development was described. Wet weight of in utero eggs and offspring size was correlated with maternal size; larger females produced larger embryos which would have higher survival rate and reproductive value. All embryos present in a female were at a similar stage of development. The external yolk sac is reabsorbed late in gestation, suggesting that embryos are mostly nourished by yolk sac reserves. Embryo size-at-birth varied considerably (180–244 mm total length) as a result of the significant variability in ova size at ovulation. The amounts of water, organic and inorganic matter of embryos at different stages of development were measured to determine possible maternal contributions during embryonic development. Total wet weight from smallest and largest in utero eggs to smallest and largest term embryos changed by +46 and +58%, respectively. This pattern was due to a change in water content by +137 and +154%, and inorganic matter by +100 and +156%. Organic matter of smallest and largest in utero eggs changed by –23 and –17%, respectively. The uterus of pregnant females became specialised for water and mineral transport, not nutrient provision. These results indicate that *S. megalops* is a strict yolk-sac viviparous species with no maternal contribution of organic matter during development.

Introduction

Maternal contribution of sharks has been studied by histological analysis of the uterus structure of pregnant females (e.g. Ranzi 1934; Jollie and Jollie 1967; Hamlett 1993) and by analysis of changes in weight and composition during embryo development. This latter approach consists of comparing the wet, dry and ash weights of the initial (fertilised ova) and final (full-term embryo) stages of embryo development (e.g. Ranzi 1932, 1934; Amoroso 1960; Wourms et al. 1988). However, given that many shark species exhibit high variability in ova size at ovulation, which is generally correlated with the size of the female, care must be taken if a small sample size is analysed (Guallart and Vicent 2001).

High variability in ova size at ovulation is reported for most dogfish species (Squaliformes) (e.g. Hanchet 1988; Yano 1995; Guallart and Vicent 2001). Hence, a representative sample is needed when maternal contribution is studied by analysis of change in weight and composition during embryo development. Ranzi (1932, 1934) reported high losses of organic matter during development of the gulper shark (*Centrophorus granulosus*) (–54%) and the spiny dogfish (*Squalus*

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acanthias) (–40%). Despite the small sample sizes used (one in utero egg and one full-term embryo for *C. granulosus*, and four embryos for *S. acanthias*), these results have been assumed accurate by later authors without further analysis of their validity (Guallart and Vicent 2001). These authors, on the other hand, adequately accounted for the high variability observed in ova size at ovulation by analysing a representative sample of *C. granulosus* embryos, for which they reported a loss of organic matter of only –18/–25% during gestation, indicating no maternal contribution. Even though sharks of the genus *Squalus* are considered yolk-sac viviparous species, most of the evidence is based on macroscopic inspections of dissected pregnant females, and, with the exception of *S. acanthias*, maternal contribution to embryo development has not been properly explored. Hence, further research is needed on the type of maternal contribution exhibited by this group.

The piked spurdog (*S. megalops*) is a very abundant shark species of southern Australia (Bulman et al. 2001; Graham et al. 2001) and one of the most commonly taken shark species in the by-catch of the gillnet and longline fisheries of this area (Walker et al. 2005). Braccini et al. (2006) have detailed the reproductive parameters needed for population assessments of this species and Watson and Smale (1998) suggested that all nutrients required for embryonic development are present in the fertilised ova. However, this was inferred from macroscopic inspections of dissected pregnant females and no thorough analysis of maternal contribution was carried out. The objectives of the present research were to: (i) study the relationship between offspring weight and maternal size; (ii) describe the embryonic development of *S. megalops*; and (iii) determine the maternal–embryo nutritional relationship.

Materials and methods

Sampling

Specimens of *S. megalops* were obtained from the by-catch of the shark and trawl sectors of the Australian Southern and Eastern Scalefish and Shark Fishery in waters off southeastern Australia between October 2002 and April 2004. Pregnant females were measured (total length, TL, ±1 mm) and dissected to remove their embryonic system (embryos and/or in utero eggs).

Embryos and in utero eggs were weighed (EMW and EGW, respectively, ±0.01 g) and, for each embryo, total length (TL_e, ±1 mm) was recorded and the external yolk sac (EYS), internal yolk sac (IYS) and liver were separated. These embryonic structures and the eviscerated embryo (EvE) were then weighed (±0.01 g).

Offspring weight–maternal size relationship

The offspring weight–maternal size relationship was determined by plotting EGW against maternal TL and, for near-term embryos, by plotting total, liver and EvE weights against maternal TL. A linear regression model was used to present these relationships. The linear relationship was adopted after inspection of scattergrams of the data. Embryos were considered near-term when the EYS was completely absorbed.

Embryo development

Embryonic development was investigated by recording the TL_e and gestation time at which fins, external gills and egg capsules were macroscopically visible and by plotting the relationships between TL_e and EYS, IYS, liver and EvE wet weights. Gestation time was determined based on a Gompertz growth model used by Braccini et al. (2006) to determine the gestation period of this species. The Gompertz growth equation is

$$L_t = L_\infty e^{-e(-k(t-t_0))},$$

where L_t is the length at gestation time t, and L_∞, k and t_0 are parameters obtained from Braccini et al. (2006).

A power function was used to represent the relationships between TL_e and liver and EvE wet weights through linear regression of log-transformed data. The power relationship was adopted after inspection of scattergrams of the data.

Maternal–embryo nutritional relationships

The wet, dry and ash weights of the embryonic system were used to determine the nutritional relationship between pregnant females and embryos. For a representative subsample of embryos, the dry weight of embryonic structures (EYS, IYS, liver and EvE) of pregnant females was obtained by drying these structures at 60°C for 45–60 days until a constant weight was reached. These samples were then incinerated at 200, 300 and 550°C to obtain the ash weights. Samples were taken to intermediate temperatures (200 and 300°C) to avoid sudden incineration and were left at 550°C for 10–15 h. From this process, water content, organic matter and inorganic matter were obtained as follows: water content = wet weight – dry weight;

organic matter = dry weight – ash weight; inorganic matter = ash weight (Guallart and Vicent 2001). Total weight of the embryonic system was considered to be the sum of EvE, liver, yolk reserves and digestive tract. The digestive tract was not collected during sampling; however, given that the values of organic and inorganic matter (as percentage of wet weight) of the different embryonic structures of *S. megalops* and *C. granulosus* were similar (see Results and Guallart and Vicent 2001), the wet, dry and ash weights of the digestive tract of *S. megalops* were backcalculated using the percentage values obtained for *C. granulosus*. The dry weight–wet weight and the ash weight–wet weight relationships were determined for the embryonic structures. These relationships were then used to calculate the dry and ash weight for each of the embryos and, hence, determine their water, organic and inorganic matter content.

The wet weight, water content weight, organic matter weight and inorganic matter weight were used in a graphical method developed by Guallart and Vicent (2001) that allows taking in account of initial variability in the size of the in utero eggs. In Guallart and Vicent's (2001) method, the relationship between the weight of the embryonic system (body plus yolk reserves) and TL_e is superimposed on the body weight (without yolk reserves)–TL_e relationship. If two parallel curves (empirically derived to enclose all of the data) are drawn, their intersection with the body weight–TL_e curve would represent the sizes and weights at which embryos, corresponding to the extremes of variability, would be born (Guallart and Vicent 2001). In utero eggs were assigned a TL_e of 0 for plotting purposes.

The method used to determine nutritional relationships between pregnant females and embryos was validated by histological inspection of the uterus structure of pregnant females. Tissue samples of uteri and oviducts containing term fetuses were immersion fixed for 12 h in 2.5% glutaraldehyde, 2.0% paraformaldehyde on 0.1 M cacodylate buffer with 0.02% picric acid. Samples were washed three times in 0.1 M cacodylate buffer and then placed in 1.0% osmium tetroxide in 0.2 M cacodylate buffer for 1–2 h at room temperature. Samples were washed three times in distilled water before rapid dehydration through progressively higher ethyl alcohol concentrations (2–3 min in each of 70, 90, 95 and 100%). Samples were then placed in 100% alcohol for 23 min periods and in 100% dry ethanol for 30 min. Tissues were transferred through two changes of epoxy-propane for 15 min each and then infiltrated in a 1:1 solution of epoxy-propane and Procure-araldite resin (Protech, QLD) for up to 24 h. After removal of excess epoxy-propane and resin, samples were embedded in pure resin and placed on a roller for 6 h. Once embedded in fresh resin, samples were incubated at 60°C for 48 h. Blocks were initially sectioned at 1 μm with a glass knife on a Leica Ultracut-S ultramicrotome and stained with toluidine blue for examination with light microscopy to evaluate tissue orientation. After locating suitable areas of the thick section, blocks were sectioned at 9 nm and placed on copper grids. After staining with uranyl acetate and lead citrate, the sections were viewed with a Philips CM10 transmission electron microscope using 4489 film. Negatives were scanned, edited in Adobe Photoshop 7.0 and stored as jpeg files.

Results

Offspring weight–maternal size relationship

A total of 135 in utero eggs of 16.2–44.4 g wet weight were collected. A linear relationship between EGW and maternal TL ($df = 1{,}133$; $F = 171.9$; $P < 0.001$) was found (Fig. 1). The wet weight of 72 near-term embryos ranged from 21.5 to 61.4 g and it also showed a linear relationship with maternal TL ($df = 1{,}70$; $F = 122.1$; $P < 0.001$) (Fig. 1). Larger females also carried embryos with heavier livers ($df = 1{,}65$; $F = 112.9$; $P < 0.001$) (Fig. 1) and heavier eviscerated bodies ($df = 1{,}47$; $F = 101.5$; $P < 0.001$) (Fig. 1). These findings indicate that larger females carry larger in utero eggs and embryos.

Embryo development

A total of 471 embryos and in utero eggs were collected for the analysis of embryonic development (Fig. 2). All embryos present in a female were in the same stage of development. In the early stage of gestation, each uterus contained 1–2 eggs (Fig. 2a) enclosed in a rigid amber capsule. Embryos 23–53 mm TL_e (140–190 gestation days) were enclosed in the egg capsule, had undifferentiated sex (based on macroscopic inspection of claspers), long filamentous external gills, developing fins, and no pigmentation (Fig. 2b). Two embryos within this size range (23 and 24 mm TL_e respectively) had no developing fins. The egg capsule degenerated and was not observed in females carrying embryos >56 mm TL_e (>194 gestation days). Transition between filamentous external gills to internal gills was observed on embryos 54–71 mm TL_e (192–214 gestation days). Also, for some of these embryos, the body and fins were pigmented. Embryos

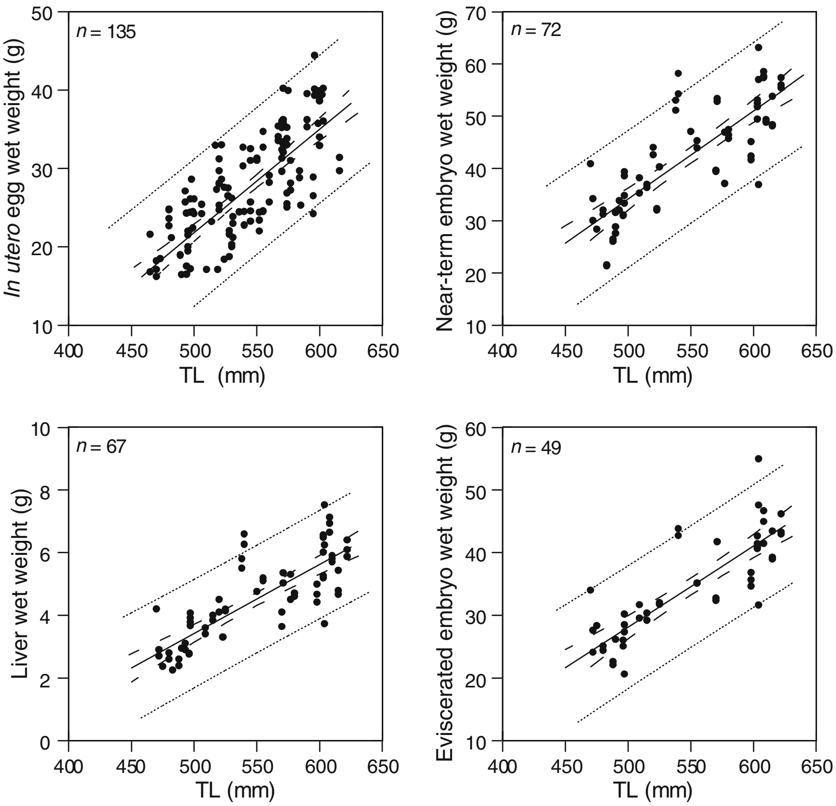

Fig. 1 Relationship between maternal total length (TL) and in utero egg wet weight (EGW), near-term embryo wet weight (EMW), near-term embryo liver wet weight and near-term embryo eviscerated body (EvE) wet weight with 95% confidence intervals (*dashed line*) and predicted intervals (*dotted line*). EGW = 0.132 TL − 44.233; r^2 = 0.56; EMW = 0.169 TL − 50.091; r^2 = 0.64; liver wet weight = 0.022 TL − 7.597; r^2 = 0.63; EvE wet weight = 0.129 TL − 36.575; r^2 = 0.68

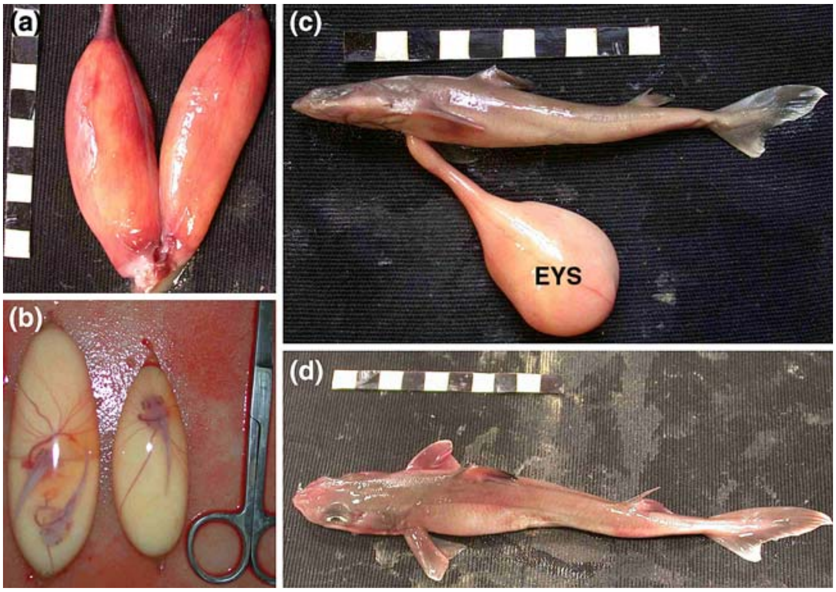

Fig. 2 Embryonic development of *Squalus megalops*. **a** In utero eggs, **b** encapsulated embryos, **c** mid-term embryo showing external yolk sac (EYS), and **d** near-term embryo. *Scale bar* 100 mm

72–77 mm TL$_e$ (215–222 gestation days) completely lost external gills and had similar pigmentation as in adults but undifferentiated sex. Sex differentiation by macroscopic observation of claspers was found for embryos >77 mm TL$_e$.

The variability observed in the weight of EYS for embryos at different stages of development and in the weight of IYS for embryos at late stage of development (Fig. 3) was similar to the variability observed for in utero eggs (Fig. 1). The EYS weight diminished with embryo growth (Figs. 2c, 3). Loss of external yolk accelerated at 172 mm TL$_e$ (370 gestation days) (Fig. 2d). Internal yolk developed at 85–115 mm TL$_e$ (233–273 gestation days). All embryos >115 mm TL$_e$

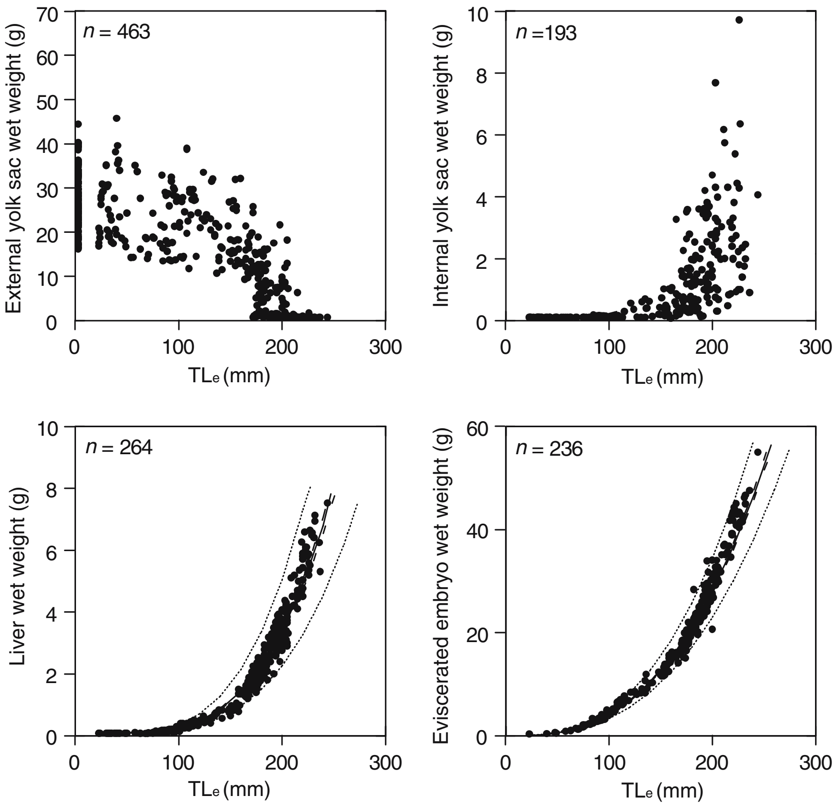

Fig. 3 Relationship between total length of embryo (TL_e) and wet weight of EYS, internal yolk sac (IYS), liver, and eviscerated embryo (EvE) with 95% confidence intervals (*dashed line*) and predicted intervals (*dotted line*). Liver wet weight = 4.59×10^{-9} $TL_e^{3.85}$; $r^2 = 0.98$; EvE wet weight = 1.10×10^{-5} $TL_e^{2.78}$; $r^2 = 0.99$. Curves are not presented for the relationship between TL_e and wet weight of external and IYSs due to the high variability of the data

had internal yolk, and this increased in weight with embryonic growth. There was a power relationship between liver wet weight and TL_e ($df = 1{,}262$; $F = 10{,}250.1$; $P < 0.001$) and between EvE wet weight and TL_e ($df = 1{,}234$; $F = 25{,}259.4$; $P < 0.001$). The exponent of the liver weight–TL_e relationship (3.85) was larger than the expected value (3) for the relationship between size and weight, suggesting that embryos are storing more reserves in the liver than expected.

Maternal–embryo nutritional relationships

A similar pattern of progression in dry weight (and hence water composition) was observed for all the embryonic structures (Fig. 4). When small (EYS and EVE <8 g wet weight, and liver and IYS <2 g wet weight), the water content was high (hence the lower dry weight) but it decreased with increasing wet weight and remained constant after the EYS and EvE attained a wet weight of ~9 g, and the liver and IYS attained a wet weight of ~3 g. Liver presented the highest values of dry weight (as % of wet weight) and hence the lowest values of water content due to its high content of squalene-rich oil. Internal and EYSs showed similar values whereas the eviscerated embryos had the lowest values of dry weight (as % of wet weight) and hence the highest values of water content.

A constant value of ash weight (as % of wet weight) was observed for most embryonic structures at ~0.6% for liver and ~1% for EYS and IYS (Fig. 4). Eviscerated embryos, on the other hand, showed an increase in ash weight (as % of wet weight) with wet weight from ~1% for smaller EvE to ~2.5% for larger EvE.

Total wet weight from smallest and largest in utero eggs to smallest and largest term embryos changed by +46 and +58%, respectively (Fig. 5). This pattern was mainly due to a change in water content by +137 and +154% and inorganic matter by +100 and +156%. Organic matter, on the other hand, changed by –23 and –17% with embryonic development. Size-at-birth, for the extremes of embryonic system variability, was determined from the intersection of the length–weight relationship with two parallel points that include all the points. Based on this method, size-at-birth was between 180 and 244 mm TL_e (Fig. 5).

Samples of term uterus and oviduct from an animal containing term fetuses were examined with transmission electron microscopy. The oviduct is bilaminar with basal sustentacular cells supporting surface epithelium. Surface cells were of two types: mucous and ciliated (Fig. 6a). Ciliated cells dominated the mucous cells which were sparsely distributed. Ciliated cells had numerous homogeneously distributed cilia with basal bodies. The nuclei of both cell types were basal and

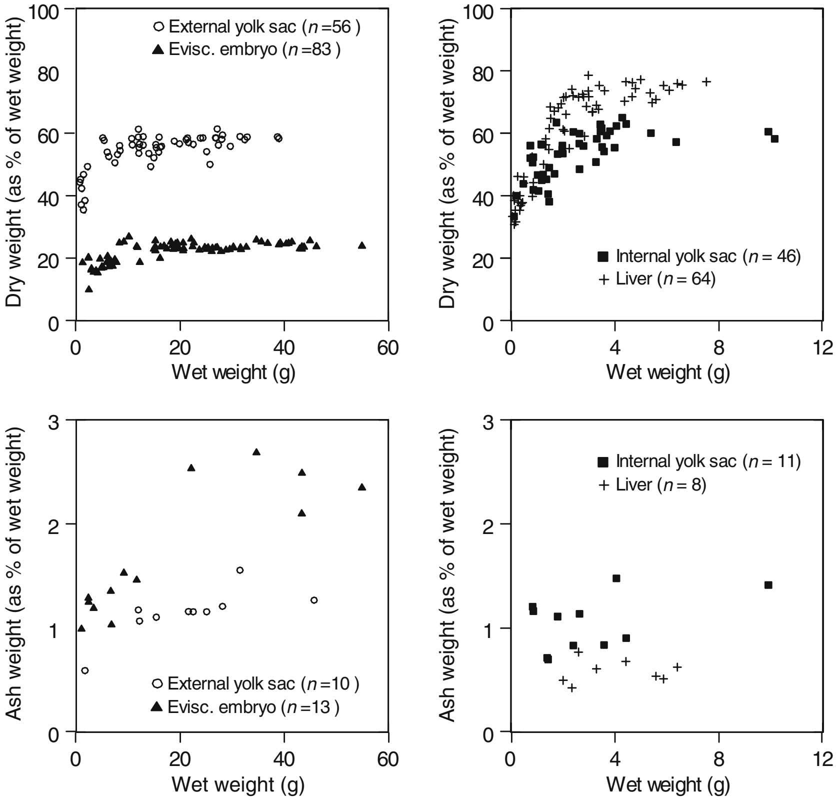

Fig. 4 Relationship between wet weight and dry weight (as percentage of wet weight) and ash weight (as percentage of wet weight) for each of the embryonic structures

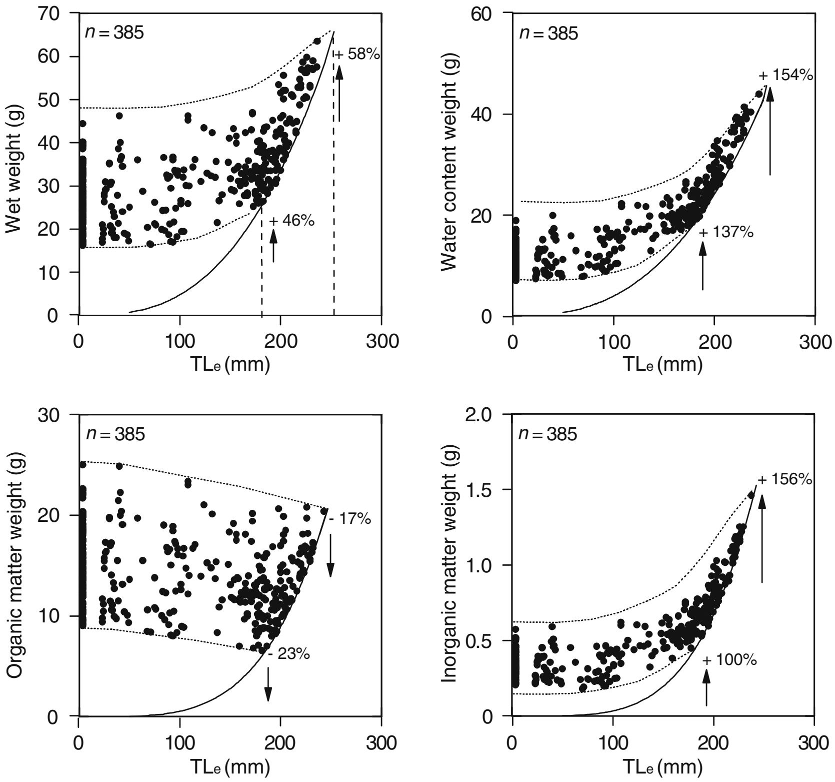

Fig. 5 Relationship between total length of embryo (TL_e) and total wet weight, total water content weight, total organic matter weight and total inorganic matter weight for embryos at different stages of development (data scattergram). The *solid line* is the body weight (without yolk reserves)–TL_e relationship. The *dotted lines* are parallel curves that include all the data points. The *vertical broken lines* indicate the size-at-birth of embryos corresponding to the extremes of variability of in utero eggs

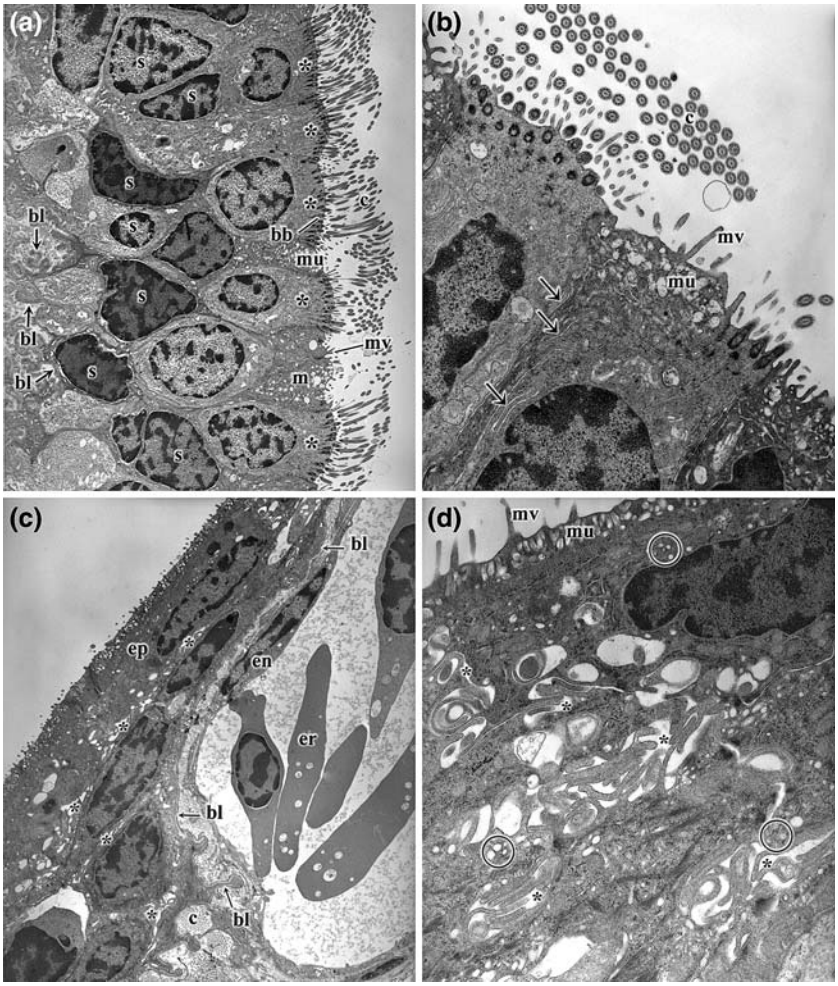

Fig. 6 Transmission electron micrographs of oviduct (**a**, **b**) and term uterus (**c**, **d**). **a** Three cell types characterise the oviduct. Sustentacular support cells (*s*) are adjacent to an undulating basal lamina (*bl*). Surface cells are mucous secretory with apical mucous droplets (*mu*) or ciliated cells (*asterisks*) with apical cilia (*c*) and basal bodies (*bb*), ×2,200. **b** Ciliated cells have apical cilia (*c*) and alternate with mucous cells with apical mucous droplets (*mu*). Lateral cell boundaries are characterised by modest plasmalemmal interdigitations (*arrows*), ×8,900 . **c** Squamous epithelial mucous cells (*ep*) are lumenal and have elaborate intercellular interdigitations (*asterisks*) with adjacent cells. Basal cells rest on a basal lamina (*bl*) adjacent to collagen bundles (*c*). Somatic endothelium (*en*) without fenestra characterises surface arterioles. *er* erythrocyte, ×2,950. **d** Surface epithelial cells have apical mucous droplets (*mu*) and scant microvilli (*mv*). Surface and underlying cells have numerous caveolae (*circles*) and elaborate intercellular plasmalemmal interdigitations and dilated intercellular space (*asterisks*), ×11,500

ovoid. Mucous cells had apical mucous droplets and sparse microvilli (Fig. 6b). Lumenally situated tight junctions sealed laterally aligned cells. Lateral cell margins with modest plasmalemmal interdigitations were found.

The term uterus consisted of flap-like folds or epithelium and mucosa with a central artery that subdivided into arterioles and capillaries. The epithelium was squamous bilaminar underlain by a continuous basal lamina (Fig. 6c). Surface cells had a modest number of microvilli and apical mucous droplets. Lateral cell boundaries were heavily interdigitated with prominent dilated intercellular spaces (Fig. 6d). Numerous transport caveolae were observed in all cells. A large sinusoid with continuous endothelium was subjacent to the epithelium.

On the lateral aspect of the uterine folds epithelial troughs were formed. Surface cells were more cuboidal and had microvilli and a large number of apical mucous droplets (Fig. 7a, b). Prominent intercellular filaments were observed.

A deeply situated muscular artery showed a continuous endothelium with many caveolae (Fig. 7c, d). Smooth muscle contained prominent plasmalemmal dense bodies as well as cytoplasmic dense bodies. The endothelium was rich in caveolae. Adjacent pericytes contained prominent rough endoplasmic reticulum and cytoplasmic filaments.

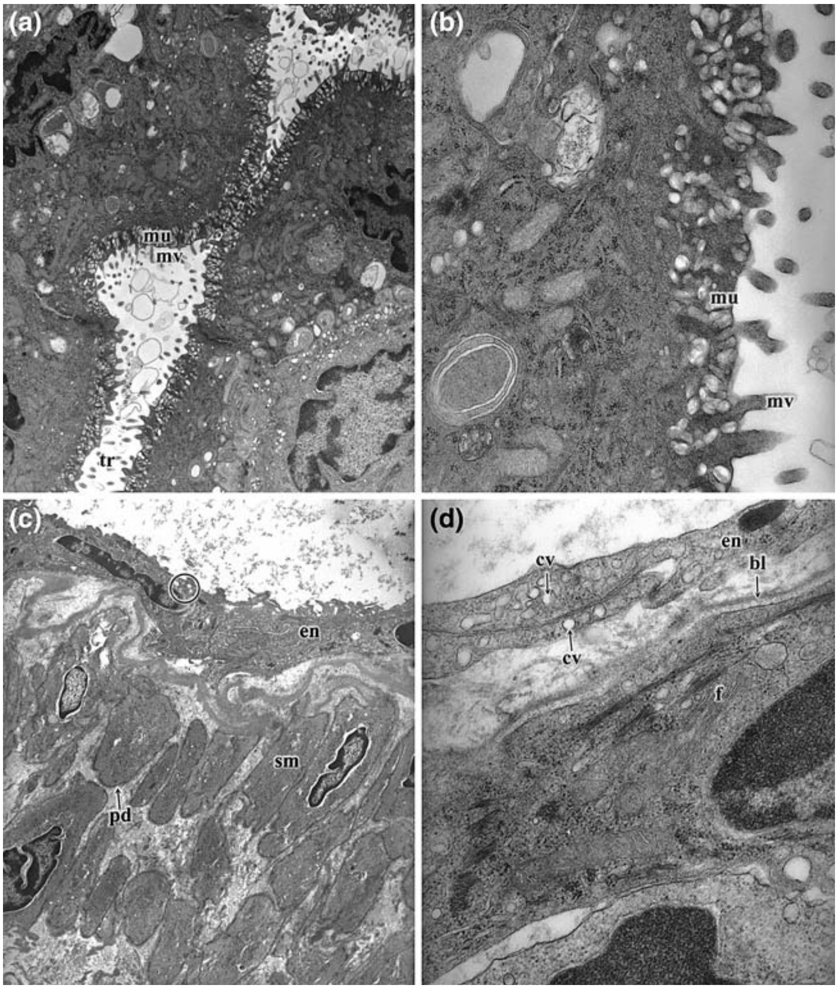

Fig. 7 Transmission electron micrographs of term uterus showing epithelial trough (**a**, **b**) and muscular arteries (**c**, **d**). Surface epithelium forms epithelial folds creating troughs (*tr*). Epithelial cells in the trough have numerous mucous droplets (*mu*) and scant microvilli (*mv*). Dilated intercellular spaces and plasmalemmal interdigitations are not as numerous as in the epithelium overlying blood vessels, **a** ×5,200 , **b** ×21,000 . **c** Muscular arteries are deeper than surface arterioles. They are characterised by somatic endothelium (*en*) without fenestra and caveolae (*circle*). Smooth muscle (*sm*) has characteristic plasmalemmal dense bodies (*pd*), ×1,650 . **d** Somatic endothelium (*en*) has numerous caveolae (*cv*) and a distinct basal lamina (*bl*). Adjacent pericytes have a rich array of cytoplasmic filaments (*f*), ×28,500

Discussion

Offspring weight–maternal size relationship

Larger female *S. megalops* produced larger in utero eggs and embryos with heavier livers and eviscerated bodies than smaller females. Similar patterns have also been reported for other elasmobranch species (e.g. Capapé et al. 2000; Seck et al. 2004). In addition, female *S. megalops* produced 1–2 embryos per uterus and only showed a slight increase in litter size with maternal total length (TL) (Braccini et al. 2006). The life history favoured by natural selection will be the one that maximises total reproductive value, a trade-off between number of embryos ('fecundity') and survivorship (Begon et al. 1990). As observed by Branstetter (1990), shark species with small litter size breed relatively large neonates. Larger embryos would have a higher reproductive value, as they are often better competitors and better at avoiding predation, and hence often have a better chance of surviving to reproduce themselves (Begon et al. 1990). Hence, larger embryos of *S. megalops* would have lower mortality rates.

Embryo development

A comprehensive sample of *S. megalops* embryos allowed a detailed description of the embryonic development of this species. At early stages of gestation, pregnant females carried one to two in utero eggs per uterus. A similar number of in utero eggs was reported for this species off New South Wales (NSW), southeast coast of Australia (Graham 2005) and South Africa (Bass et al. 1976; Watson and Smale 1998). In utero eggs were enclosed in an elongated egg case (candle case) and the initial part of development occurred inside this capsule. Other *Squalus* species, such as *S. acanthias*, the Japanese spurdog (*Squalus japonicus*), the shortspine spurdog (*Squalus mitsukurii*), and the longnose spurdog (*Squalus blainville*), also carried in utero eggs in a single egg capsule per uterus (Ford 1921; Hisaw and Albert 1947; Capapé and Quignard 1980; Chen et al. 1981). After a gestation period of ~190 days, the capsule broke open and *S. megalops* embryos were released into the uteri. A similar period of embryo encapsulation is reported for *S. acanthias* (Jones and Geen 1977).

The progression in weight of the different embryonic structures of *S. megalops* was similar to the embryonic development of other dogfish species (Jones and Geen 1977; Guallart and Vicent 2001; Veríssimo et al. 2003). Embryo growth concurred with external yolk depletion as yolk platelets are moved from the EYS into the intestine (Wourms 1977). For a matrotrophic viviparous shark, such as the gummy shark (*M. antarcticus*), in utero eggs are comparatively small and the wet mass of the EYS depletes rapidly during the early stages of gestation (T. I. Walker, unpublished data). Conversely, complete absorption of the EYS of *S. megalops* embryos occurred at late gestation, suggesting that embryos are mostly nourished by yolk sac reserves. For other lecithotrophic viviparous dogfish, EYS is also depleted at late gestation (Ketchen 1972; Guallart and Vicent 2001). At ~230 gestation days an IYS is developed where yolk is temporarily stored before passing to the intestine. The IYS weight increased with embryo growth and reached its maximum in near-term embryos, suggesting that embryos are born with yolk reserves in the internal sac. Other dogfish species are born with yolk reserves in the internal sac (e.g. Bass et al. 1976; Jones and Geen 1977; Yano 1995), although the internal yolk of full-term embryos of *S. japonicus* is almost fully absorbed (Chen et al. 1981). As proposed by Yano (1995), yolk reserves of neonates would nourish them during the first few days after birth until they become successful predators. Further nourishment for *S. megalops* neonates would be provided by the liver. This organ would be storing more energy reserves than expected given that the exponent of the relationship between liver weight and embryo total length was larger than the expected cubic value for this type of power relationship.

Size-at-birth of *S. megalops* varied considerably (180–244 mm TL_e). A wide range of size-at-birth was also reported for this species off NSW (Graham 2005) and South Africa (Watson and Smale 1998) and for several other dogfish species (Ketchen 1972; Chen et al. 1981; Yano 1995; Guallart and Vicent 2001). This general pattern of the reproductive biology of dogfishes is related to significant variability in ova size at ovulation, which is correlated with maternal size.

Maternal–embryo nutritional relationships

Changes in weight and composition for embryos of *S. megalops* indicate that females do not supplement yolk reserves during embryonic development. Yolk-sac viviparity is considered the plesiomorphic mode of reproduction of sharks and rays (Musick and Ellis 2005). For lecithotrophic species, yolk produced by the maternal liver is the only source of embryonic nutrition. For these species, a dry weight loss of an order of 20% is reported during development (Hamlett et al. 2005). In contrast, matrotrophic species, where maternal organisms supplement yolk from other sources (e.g. uterine secretions, ova, siblings or placental transfer), show a dry weight gain during development (Hamlett et al. 2005). Hence, dry weight gain or loss has been used as evidence of organic matter transfer and maternal nutrient supply during development. Given that water and minerals are incorporated into the embryo during development, comparisons based only on total dry weight can yield misleading figures. Thus, changes in organic content derived from dry weights should also include water and ash content for proper characterisation of reproductive mode. However, reliable organic matter weight or even dry weight data between in utero eggs and term embryos are lacking for most sharks (Hamlett et al. 2005).

A standard value of organic transfer in viviparous sharks has been inferred from oviparous species. Based on values obtained for the small-spotted catshark (*Scyliorhinus canicula*), Ranzi (1932) proposes that diminution in organic matter in viviparous species is ~20% as a result of energy utilisation in converting yolk to tissue and basal metabolism. Mellinger et al. (1986) and Delhaye et al. (1992) report similar figures of organic matter loss for the same species. Wourms et al. (1988), on the other hand, based on previous studies, suggest a reference value of organic matter loss of 35%. The only reliable analysis of organic matter dynamics during development of viviparous sharks is that of Guallart and Vicent (2001). These authors report a change in organic matter of –25/–18% for embryos of *C. granulosus*. Hamlett et al. (2005) reviewed the methods of quantification of lecithotrophy and matrotrophy and propose a value of –20% for oviparous and strictly lecithotrophic species. *Squalus megalops* showed a change in organic matter of –23/–17% during embryonic development. Hence, based on the values of organic matter loss, this shark is strictly lecithotrophic with no maternal contribution of organic matter.

The lecithotrophic mode of reproduction of *S. megalops* is further supported by the relatively moderate increase in wet weight during development, the large size of the ovarian follicles at ovulation (Braccini et al. 2006) and the uterus ultrastructure of pregnant females. Considerable wet weight gain from egg to full-term embryo suggests maternal contribution to embryos (Hamlett et al. 2005). Although total wet weight increased during embryonic development, the increase was due to an incorporation of water and inorganic matter from the environment. Also, the relative increase in total wet weight of embryos *S. megalops* is not as remarkable as in matrotrophic species (e.g. 3,000 fold increase in total wet weight during development in species with histotrophy, such as stingrays; Hamlett et al. 2005).

Female *S. megalops* carried large ovarian follicles at ovulation (Braccini et al. 2006). These follicles are larger in relative and absolute terms than those from most matrotrophic shark species (e.g. Yano 1993; Francis and Stevens 2000). Large ovarian follicles at ovulation are also reported for *C. granulosus* (Guallart and Vicent 2001), as yolk stored within these structures is the only source of embryo nourishment.

The uterine epithelium of female *S. megalops* in late gestation was reduced to a squamous bilayer. These cells were immediately underlain by numerous dilated vessels. Prominent intercellular spaces and numerous transport caveolae in the luminal epithelium and the vessel endothelium suggest water and mineral transport (Berridge and Oschman 1972). As for other species with yolk-sac viviparity (Hamlett et al. 2005), the design of the uterus of *S. megalops* also included longitudinal folds to increase surface area. Therefore, these characteristics make the uterus of this species a specialised structure for water and mineral transport, but not for nutrient provision.

In conclusion, wet weight of in utero eggs and offspring size was correlated with maternal size. Hence, larger females produced embryos with higher reproductive value. A comprehensive sample of embryos allowed a detailed analysis of embryonic development of *S. megalops* where the significant stages of development were described. Finally, based on the values of organic matter loss during development, the large ovarian follicles at ovulation, a late depletion of EYS of embryos and the uterus ultrastructure of pregnant females, *S. megalops* is considered a strict yolk-sac viviparous species with no maternal contribution of organic matter during development.

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Comparison of deterministic growth models fitted to length-at-age data of the piked spurdog (*Squalus megalops*) in south-eastern Australia

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Abstract. Age and growth estimates of *Squalus megalops* were derived from the first dorsal fin spine of 452 sharks, ranging from 274 to 622 mm total length. Age bias plots and indices of precision indicated that the ageing method was precise and unbiased. Edge analysis of the enameled surface of whole spines and similarities in the banding pattern deposited in the enameled surface of spines and in spine sections supported the hypothesis of annual band formation. Multiple versions of two growth models were fitted to length-at-age data, from which a two-phase von Bertalanffy model produced the best fit. For males, the change in growth rate corresponded with size-at-maturity, whereas for females, the change was slightly before size-at-maturity. Regardless of the growth model used, growth rate of females (0.034 to 0.098 years^{-1}) was very low, making *S. megalops* highly susceptible to overexploitation by fisheries.

Additional keywords: age, AIC, Gompertz, Squalidae, von Bertalanffy.

Introduction

The von Bertalanffy function (von Bertalanffy 1938) has been the most commonly used model to describe growth of sharks, despite criticism (Knight 1968; Roff 1980). As indicated by Carlson and Baremore (2005), few studies on shark growth have examined alternative models (but see Carlson and Baremore 2005; Bishop *et al.* 2006), and most studies simply fitted the von Bertalanffy function to the data. Hence, a range of growth models should be compared to determine the function that provides the best description of the growth process (Haddon 2001).

Age and growth rates have been mainly studied for commercially important sharks, such as spiny dogfish *Squalus acanthias*, gummy sharks *Mustelus antarcticus* and school sharks *Galeorhinus galeus*; however, little is known about the age and growth of non-commercial squalid sharks (Squalidae). Although dogfish are among the most abundant demersal sharks of temperate seas (Compagno 1984), most of the ageing studies on this family have focused on *S. acanthias* (e.g. Holden and Meadows 1962; Ketchen 1975; Beamish and McFarlane 1985). For this species, maximum age was reported to vary widely, with a reported maximum age of up to 80 years (McFarlane and Beamish 1987). For other species of *Squalus*, age and growth rate have been estimated for the shortspine spurdog *S. mitsukurii* in the North Pacific Ocean (Wilson and Seki 1994; Taniuchi and Tachikawa 1999) and the longnose spurdog *S. blainvillei* in the Mediterranean Sea (Cannizzaro *et al.* 1995). Age and growth rate information of the piked spurdog *S. megalops* was estimated for sharks from South African waters (Watson and Smale 1999). Growth rates and maximum ages differed between males and females: the largest male was 572 mm total length (TL) and 29 years old, whereas the largest female was 782 mm TL and 32 years old.

Squalus megalops (Macleay, 1881) is a demersal species that is distributed off southern and eastern Australia, from Carnarvon (Western Australia) to Townsville (Queensland), including Tasmania (Last and Stevens 1994). However, the distribution of this species requires further revision because it has also been reported off the coasts of Brazil (Vooren 1992) and South Africa (Bass *et al.* 1976), and there are unconfirmed reports off Indo China, New Caledonia and New Hebrides (Last and Stevens 1994). This species inhabits the continental shelf and upper continental slope (depths <510 m) in warm, temperate and tropical areas (Last and Stevens 1994). *Squalus megalops* has a high natural abundance in southern Australia (Bulman *et al.* 2001; Graham *et al.* 2001) and, even though it is one of the major by-catch shark species in the area (Walker *et al.* 2005), its abundance has remained stable off New South Wales (south-east coast of Australia) since it was first surveyed in 1976–77 (Graham *et al.* 2001). At present, a lack of biological data hampers a classification of the conservation status of this species (Cavanagh *et al.* 2003).

Until the present study, the age and growth rate of the Australian population(s) of *S. megalops* remained unknown. Given that age and growth parameters can vary among regions (e.g. Parsons 1993; Taniuchi and Tachikawa 1999), age and growth information for *S. megalops* from Australian waters is required for population assessment of this species in this region. The

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purpose of the present study was to estimate the age of *S. megalops* captured in south-eastern Australia and compare different growth models to determine which model provides the best fit to growth data.

Materials and methods

Sampling

Specimens of *Squalus megalops* were obtained from the by-catch of demersal trawl and shark gill-net vessels operating in the Southern and Eastern Scalefish and Shark Fishery in waters off south-eastern Australia. Samples were collected monthly between October 2002 and April 2004, with the exception of the August-September period, when *S. megalops* appeared to move off the fishing grounds and weather conditions restricted sampling. Specimens were sexed and measured (total length, TL, ± 1 mm).

Spine and vertebrae preparation

Two portions of the vertebral column (post cranial and thoracic vertebrae) and the first and second dorsal fin spines (DFS) were removed and stored frozen for age estimation. Spines were extracted by cutting horizontally just above the vertebral column to ensure that the spine base and stem were intact (Beamish and McFarlane 1985). Soft tissue was removed by immersing vertebrae and spines in hot water (55°C) for 0.5 to 1 min and trimming off the skin, flesh, and cartilage with a scalpel. Cleaned spines were then rubbed with a cloth to highlight the bands on the enameled surface. For vertebrae, the remaining tissue was removed by soaking them in 4% sodium hypochlorite solution. Soaking time varied with the size of the vertebrae (between 10 and 20 min) to avoid 'over-bleaching'. Spines were air-dried and stored in paper envelopes, whereas vertebrae were stored in a freezer. Measurements of spines were recorded to the nearest 0.01 mm using electronic calipers, following Ketchen (1975) (Fig. 1*a*).

Age estimation

A pilot study was conducted to determine which of the two structures – vertebrae or spines – was more appropriate for age estimation. Whole and cross-sectioned vertebrae (~300 μm) were used. Sections were obtained by embedding vertebrae in epoxy resin and sectioning with a lapidary saw (Gemmasta, Adelaide) with a diamond-impregnated blade. Sections were cleaned using ethanol and water, air-dried and mounted on glass slides using epoxy resin. Sections were examined under transmitted light using a Leica IM 4.0 digital image system (Leica, Wetzlar, Germany) on a Leica DMLB compound microscope. Vertebrae of *S. megalops* are poorly calcified, with very fragile *intermedialia*; therefore, from sectioned vertebrae, only the *corpus calcareum* was used. No clear banding pattern was observed on whole or sections of vertebrae; hence, different stains (alizarin red S, silver nitrate, cobalt nitrate, ninhydrin) were used to enhance readability. However, no improvement in readability was observed, and subsequently only spines were used for further age estimation.

Bands deposited on the external enameled surface of spines were counted using a dissecting microscope (10×) and reflected light (Fig. 1*b*). A band was defined as an alternating opaque and translucent zone or ridge present on the enameled surface (McFarlane and Beamish 1987; Watson and Smale 1999). Solid bands on the leading edge of the spine that were split on the trailing edge were counted as a single band (Watson and Smale 1999). Bands visible only as a dark mark on the leading edge,

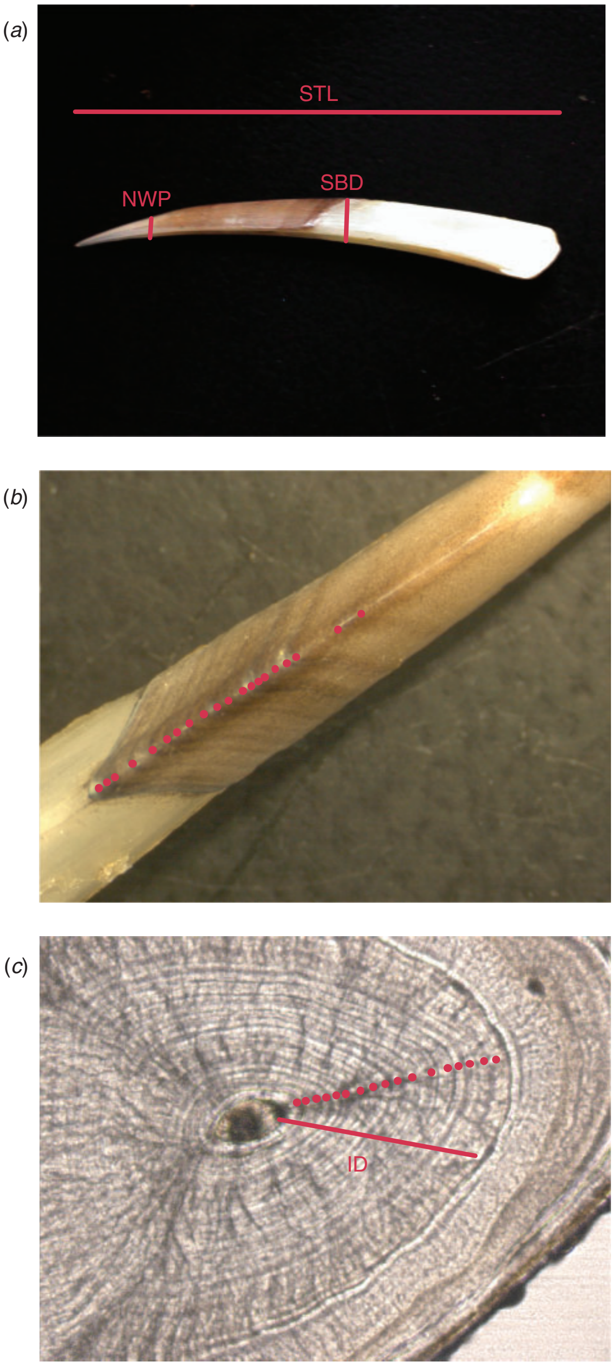

Fig. 1. Dorsal fin spine (DFS) of *Squalus megalops*. (*a*) Lateral view of worn second DFS showing the different measurements recorded following Ketchen (1975); STL, spine total length; SBD, spine-base diameter; NWP, no-wear point. (*b*) Anterior view of the first DFS of a 495 mm TL female showing 20 bands on the enameled surface (6×). (*c*) Section of the first DFS of a 456 mm TL female showing 17 bands on the inner dentine (ID) layer (100×).

Table 1. Readability scores assigned to readings of spines
(modified from Officer *et al.* 1996)

Readability score	Description
1	Band count unambiguous with clear bands
2	Band count unambiguous but bands of diminished clarity
3	Two band counts possible but indicated count is most likely
4	More than two interpretations possible; count is best estimate
5	No band count possible; unreadable

Table 2. Definition of edge type of whole spines for edge analysis
(following Holden and Meadows 1962)

Edge type	Description
Dark	Dark band observed at edge of enamel
Light	Dark band just formed and a light band of a width less than half the width of the light band between the last two dark bands observed at edge of enamel
Wide light	Light band observed at edge of enamel, equal to or more than half the width of the light band between the last two dark bands

but similar in thickness to neighbouring bands that did continue to the trailing edge, were also counted as single bands (Watson and Smale 1999). A subjective readability score was assigned to each spine following Officer *et al.* (1996) (Table 1). After three readings, spines with a readability score of 4 (ambiguous band counts) or 5 (no band counts possible) were not used for further analysis.

The spines of ten full-term embryos were examined to determine pre-birth bands. No bands were observed, and it was assumed that the first band was deposited just prior to or after birth (birthmark; e.g. Holden and Meadows 1962; Moulton *et al.* 1992). Thus, the final band count was calculated as the total number of bands counted minus one.

To determine whether the first or the second DFS was more appropriate for age estimation, a random sub-sample of first and second DFS from 61 individuals was read on two occasions (separated by a minimum of one month) without knowledge of the length of the specimens. The readability scores of the first and second DFS were compared. The coefficient of variation (CV; Chang 1982) and the index of average percentage error (APE; Beamish and Fournier 1981) were calculated to evaluate precision between readings (first *v.* second reading) and between structures (first *v.* second DFS). Age-bias plots (Campana *et al.* 1995) were used to detect count differences between the two structures. The first DFS showed better readability scores and higher precision between readings (see 'Results'); hence, this spine was used for age estimation.

All first DFS were read three times by a single reader (first reader), with a time period of at least one month separating the readings. A second reader read a random sub-sample of 50 spines for evaluation of between-reader variability and between-reader bias. To evaluate within- and between-reader precision, the CV and APE index were calculated. Age bias plots were used to detect systematic count differences between the first and second reader. To accept a count for age estimation, the counts of at least two of three readings had to be identical. If counts differed, spines were recounted a fourth time and the same procedure was applied. If the difference persisted, the spine was discarded ($<9\%$ of readings).

For worn spines, Ketchen's (1975) correction method was adopted to ensure that bands were not missing. The relationship between band counts and spine-base diameter (SBD) was estimated for unworn spines from males ($n = 45$) and females ($n = 46$). For worn spines, the diameter of the spine at the most distal point of no wear (NWP) was then measured (Fig. 1*a*). From the relationship between band counts and SBD, the number of bands corresponding to the diameter at the NWP of worn spines was calculated and added to the original count of bands (Ketchen 1975).

Verification

A random sub-sample of spines from 10 female and 10 male sharks was sent to G. A. McFarlane from the Pacific Biological Station, and to G. Watson and M. J. Smale from Port Elizabeth Museum at Bayworld, who agreed that the spines were appropriate to estimate the age of *S. megalops*. The annual periodicity of band deposition on whole spines was investigated by analysing the edge of their enameled surface (Holden and Meadows 1962; Nammack *et al.* 1985; Taniuchi and Tachikawa 1999). The edge of spines collected throughout the year was classified as dark, light or wide light following Holden and Meadows (1962) (Table 2).

Counts on spine sections were compared with counts on the external enameled surface for a sub-sample of sharks ($n = 89$) as a second form of verification. Serial sections ($\sim 300\,\mu\text{m}$) were taken from the tip of each first DFS to determine the optimal position of sectioning. The same method for sectioning vertebrae was used to obtain spine sections. The inner dentine layer exhibited the clearest banding pattern and was hence used for counting (Fig. 1*c*) (Maisey 1979; Clarke *et al.* 2002*a*). Maximum count of bands in the inner layer was found at the apex

Table 3. Summary of growth models fitted to length-at-age data

Model	Equation
VBGM	$L_t = L_\infty(1 - e^{-k(t-t_0)})$
2VBGM	$L_t = L_\infty(1 - be^{-kt})$, $b = (L_\infty - L_0/L_\infty)$
TPVBGM	$L_t = L_\infty(1 - e^{-kA_t(t-t_0)})$, $A_t = 1 - h/((t - t_h)^2 + 1)$
Gompertz	$L_t = L_\infty e^{-e^{(-k(t-t_0))}}$
2Gompertz	$L_t = L_0 e^{G(1-e^{-kt})}$, $G = \ln(L_\infty/L_0)$

VBGM, von Bertalanffy growth model; 2VBGM, two-parameter modified VBGM; TPVBGM, two-phase VBGM; 2Gompertz, two-parameter modified form of the Gompertz growth model; L_t, mean length at time t; L_∞, theoretical asymptotic length; k, growth coefficient; t_0, theoretical age at zero length; h, magnitude of the maximum differences between VBGM and TPVBGM; t_h, age at which transition between the two growth phases occurs; L_0, mean length at birth (214 mm for males and females).

of the pulp cavity, representing the optimal position of sectioning. The sections were examined under transmitted light using a Leica IM 4.0 digital image system on a Leica DMLB compound microscope. Within the internal dentine layer, a band was defined as a pair of dark (opaque) and light (translucent) concentric rings (Irvine 2004). Counting started at the pulp cavity (centre) and continued outwards to the junction between inner and outer dentine layers (Irvine 2004). Age-bias plots (Campana *et al.* 1995) were used to detect count differences between external (enameled surface) and internal (sections) counts.

Growth estimation

Several alternative growth models were fitted to length-at-age data for each sex: the traditional von Bertalanffy growth model (VBGM; von Bertalanffy 1938), a two-parameter modified form of VBGM (2VBGM; Fabens 1965), a two-phase von Bertalanffy growth model (TPVBGM; Soriano *et al.* 1992), the Gompertz growth model (Ricker 1975), and a two-parameter modified form of the Gompertz growth model (2Gompertz; Mollet *et al.* 2002) (Table 3). Model parameters were estimated by least-squares non-linear regression. Akaike's Information Criterion (AIC) was used to determine the model that provided the best fit to the length-at-age data (Buckland *et al.* 1997; Burnham and Anderson 2002)

$$\mathrm{AIC} = n\ln(\hat{\sigma}^2) + 2p$$

where n is sample size; $\hat{\sigma}$ is residual sum of squares divided by n; and p is number of parameters.

Comparisons among the AIC values of different growth models enabled the best model for each sex to be selected, i.e. those models with the lowest AIC values. For model comparisons, the ΔAIC and Akaike weights (w_i) were calculated. The ΔAIC is a measure of each model relative to the best model and is calculated as

$$\Delta\mathrm{AIC} = \mathrm{AIC}_i - \mathrm{minAIC} \qquad (1)$$

where AIC_i = AIC value of model i; and minAIC = AIC value of the best model.

Akaike weights (w_i) represent the probability of choosing the correct model from the set of candidate models and are calculated as

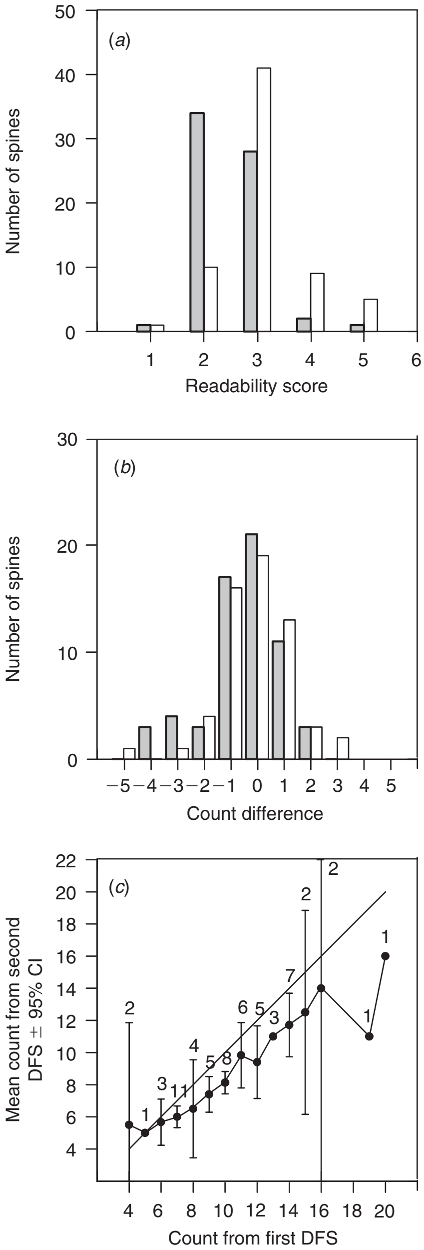

Fig. 2. Comparison between first (grey) and second (white) dorsal fin spines (DFS) for 61 sharks. (*a*) Distribution of readability scores assigned to readings of each spine. (*b*) Distribution of differences between two readings on first and second DFS. (*c*) Age bias plots. The solid line is the 1:1 relationship. Sample sizes are given above each corresponding count.

$$w_i = \frac{\exp(-\Delta\mathrm{AIC}/2)}{\sum_{r=1}^{R}\exp(-\Delta\mathrm{AIC}/2)}$$

where R is the number of candidate models.

Once the best model was determined, the growth curves of males and females were compared by a χ^2 test on likelihood ratios (Kimura 1980; Cerrato 1990).

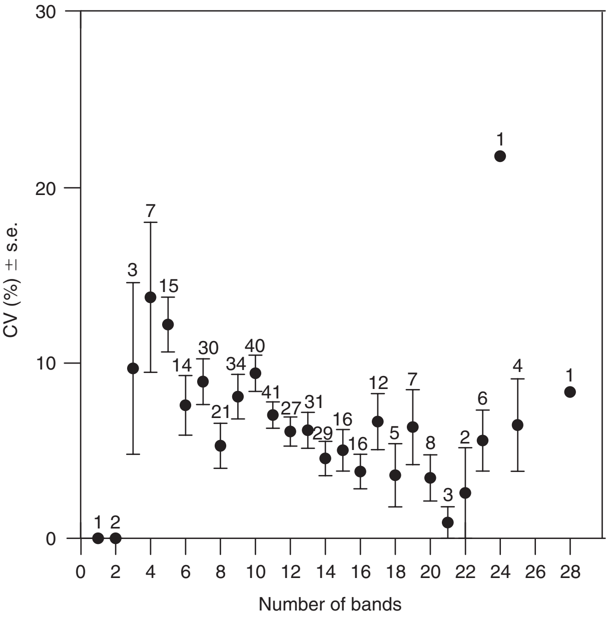

Fig. 3. Mean (± s.e.) values of coefficient of variation (CV) for each band class read by the principal reader. Sample sizes are given for each corresponding band class.

Results

Age estimation

The first dorsal fin spines (DFS) provided better readability scores and more precise readings than the second DFS. Most first DFS had a readability score of 2 (51.5%) or 3 (42.4%), whereas most of the second DFS had a readability score of 3 (62.1%) or greater (Fig. 2*a*). Differences between readings for first and second DFS varied by up to five bands, but differences were mostly ±1 count (Fig. 2*b*). Mean coefficient of variation (CV) and index of average percentage error (APE) among readings were 7.53 and 5.33%, respectively, for the first DFS and 9.03 and 6.39%, respectively, for the second DFS, indicating that more precise counts were obtained when the first DFS was used. Mean CV and APE between the first and second DFS were 14.04 and 9.93% respectively. Agreement between first and second DFS decreased with the number of bands counted (Fig. 2*c*). The first DFS was used for age estimation because it showed a clearer readability pattern, higher precision between readings, and an overall higher number of bands.

The relationship between the first DFS length and total length was linear (DFS length = 0.086 total length [TL] − 2.739, $r^2 = 0.9$) and there was no significant difference between males and females (Student's *t*-test, $t = 1.77$, d.f. = 98, $P > 0.05$ for comparison of slopes, and $t = 1.07$, d.f. = 98, $P > 0.05$ for comparison of elevations). The increase in DFS length with total length shows that spines grow throughout life, indicating that this structure is useful for age estimation.

A total of 493 first DFS were examined, of which 41 (8.3%) were rejected because they did not conform to the selection criteria (i.e. readability score ≤ 3 and identical counts from at least two of three or four readings). Band counts from 163 males (274 to 470 mm TL) and 289 females (287 to 622 mm TL) were used for age estimation. Within-reader precision among readings (sexes combined) was high: mean CV and APE were 6.99 and 4.94% respectively. Overall, for each band class, CV was low, exhibiting the lowest values for mid-band classes (14 to 23 band class) (Fig. 3). Mean CV and APE between readers (sexes combined) were 11.35 and 8.03% respectively. There were no systematic differences between readers (Fig. 4). Worn spines (4.9% for males and 15.9% for females) were corrected for missing bands using the equations derived from the relationship between the number of bands and spine-base diameter (SBD) of unworn spines ($\text{Counts}_{\text{male}} = 0.394\text{SBD}^{3.064}$, $r^2 = 0.83$; $\text{Counts}_{\text{female}} = 0.965\text{SBD}^{2.083}$, $r^2 = 0.94$).

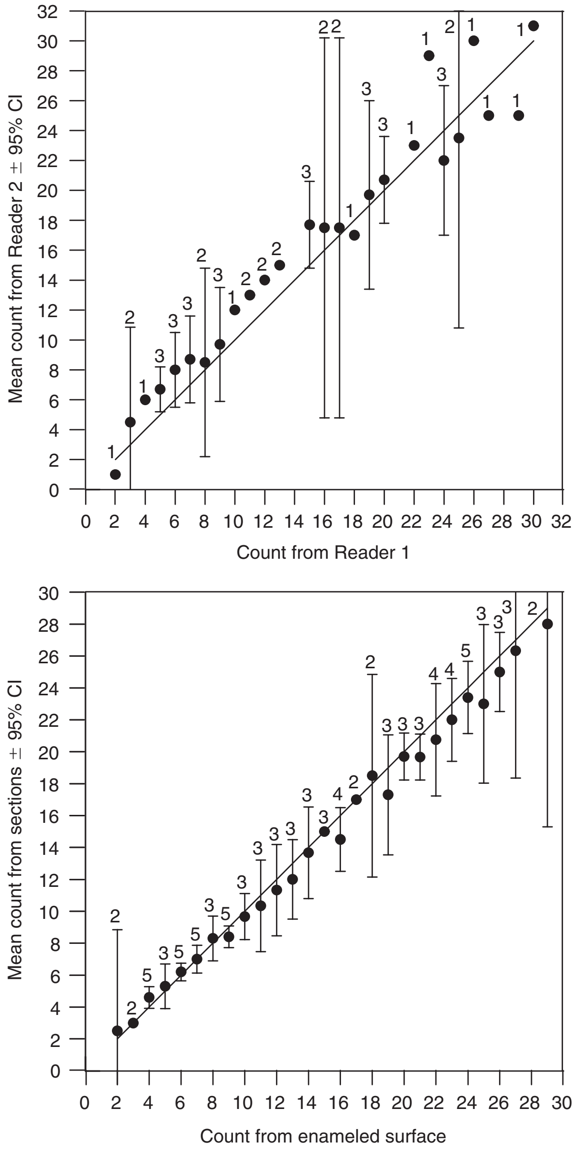

Fig. 4. Age-bias plot for the comparison of band counts between readers and band counts on spine sections and on the external enameled surface. The solid line is the 1:1 relationship. Sample sizes are given above each corresponding count.

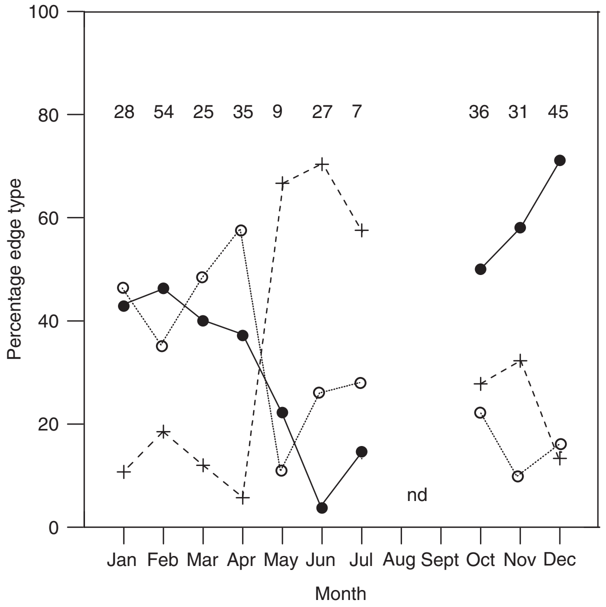

Fig. 5. Monthly variation in the type of enamel edge. White circle: wide light edge (WL); black circle: light edge (L); +: dark edge (D); nd, no data. Sample sizes are given for each corresponding month.

Verification

The nature of the enamel edge varied with month (Fig. 5). At no time of the year were the spines entirely of one edge type. Most sharks collected between May and July (autumn-winter) had dark edges, whereas the highest percentage of light edges occurred in sharks collected between October and December (spring-early summer). For spines with wide light edges, the highest percentage was found in sharks collected between January and April (summer-autumn). This annual edge pattern suggests that dark rings form during the cold period of the year. In addition, there was good agreement between counts on spine sections and counts on the external enameled surface (Fig. 4).

Growth estimation

Males ranged from 1 to 15 years in age, whereas females reached a maximum age of 28 years. Most males were 11 to 12 years old, whereas most females were 13 to 14 years (Fig. 6). Growth parameters of *Squalus megalops* were estimated separately from five models fitted to length-at-age data (Table 4). Growth models fitted the data well, with females showing higher coefficients of determination ($r^2 \geq 0.88$) than males ($r^2 \geq 0.72$).

For males, the two-phase von Bertalanffy growth model (TPVBGM) was the best of the growth models fitted with an Akaike weight (w_i) of 0.54 (Table 4). However, the von Bertalanffy (VBGM) and Gompertz growth model followed rather closely ($w_i = 0.24$ and 0.19 respectively), revealing a degree of uncertainty regarding the best model for fitting length-at-age data of males. The TPVBGM predicted values (and 95% confidence intervals) of asymptotic lengths (L_∞) and growth coefficients (k) of 455 (19) mm TL and 0.158 (0.05) years^{-1} respectively.

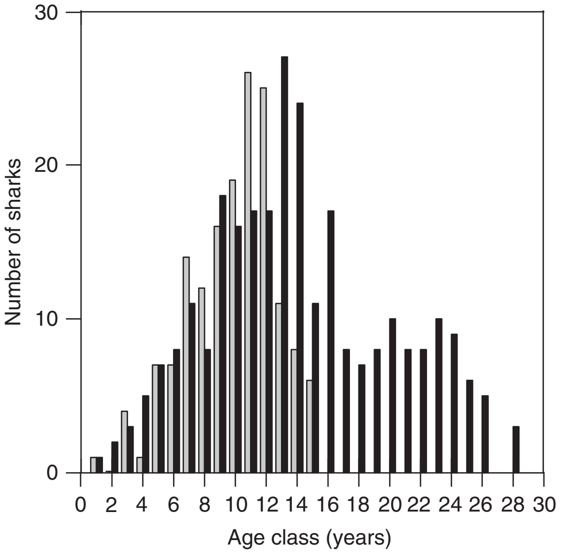

Fig. 6. Age distribution for male (grey) and female (black) *Squalus megalops*.

For females, the best fitting model was the TPVBGM with a w_i of 0.95 (Table 4); other models gave lower values of w_i, indicating that they do not fit the length-at-age data as well. The TPVBGM predicted values (and 95% confidence intervals) of L_∞ and k of 756 (88) mm TL and 0.042 (0.01) years^{-1} respectively.

The TPVBGM provided the best fit for females and a better fit than other models for males; therefore, this function was used to construct the growth curves for both sexes (Fig. 7). Likelihood ratio tests indicated significant differences between the growth curves of the two sexes ($P < 0.001$). Males grew faster than females (Table 4). Predicted length-at-age of males was initially higher, but after they attained eight years of age, growth of males and females was similar up to ~10 years when transition between growth phases occurred (Fig. 7; Table 4). After age 10, growth of males slowed down whereas growth of females continued with length, increasing steadily throughout their lifespan.

Discussion

The first dorsal fin spines (DFS) of *Squalus megalops* showed clearer readability, higher precision between readings and an overall higher number of bands than the second DFS. Most ageing studies on squalid sharks use whole second DFS because it is larger and the tip of the first DFS tends to be worn down (Cailliet and Goldman 2004). Although some studies have used the first DFS as a check (e.g. Nammack *et al.* 1985), few have compared the suitability of the first and second DFS for ageing (but see Holden and Meadows 1962; Irvine 2004). Given that the structure of the first and second DFS is similar (e.g. Holden and Meadows 1962; Clarke *et al.* 2002*a*), preference for first or second DFS for age estimation should be a question of readability. Sections of the first DFS of the birdbeak dogfish *Deania calcea* (Clarke *et al.* 2002*a*) and the gulper shark *Centrophorus squamosus* (Clarke *et al.* 2002*b*) provided better readability than sections from the second DFS. For *S. megalops*

Table 4. Growth estimates (with 95% confidence intervals) and model selection criterion for male and female *Squalus megalops*
Refer to Table 3 for meaning of parameters

Model	Parameter	Estimate	Males ($n = 157$)				Estimate	Females ($n = 274$)			
			r^2	AIC	ΔAIC	w_i		r^2	AIC	ΔAIC	w_i
VBGM	L_∞ (mm)	455 (21)	0.74	851.85	1.68	0.24	829 (126)	0.89	1774.94	9.50	0.01
	k (years^{-1})	0.144 (0.05)					0.034 (0.01)				
	t_0 (years)	−5.72 (2.50)					−10.83 (2.82)				
2VBGM	L_∞ (mm)	440 (9)	0.73	856.19	6.02	0.03	699 (33)	0.88	1791.11	25.68	<0.01
	k (years^{-1})	0.198 (0.02)					0.056 (0.01)				
TPVBGM	L_∞ (mm)	455 (19)	0.75	850.17	0	0.54	756 (88)	0.89	1765.43	0	0.95
	k (years^{-1})	0.158 (0.05)					0.042 (0.01)				
	t_0 (years)	−4.86 (2.10)					−9.77 (2.60)				
	h	0.094 (0.08)					0.087 (0.05)				
	t_h (years)	10.5 (0.60)					10.2 (0.60)				
Gompertz	L_∞ (mm)	449 (17)	0.74	852.27	2.10	0.19	717 (59)	0.89	1771.92	6.49	0.04
	k (years^{-1})	0.172 (0.05)					0.063 (0.01)				
	t_0 (years)	−3.54 (1.68)					0.026 (0.81)				
2Gompertz	L_∞ (mm)	433 (7)	0.72	861.11	10.94	<0.01	632 (18)	0.88	1804.37	38.90	<0.01
	k (years^{-1})	0.252 (0.02)					0.098 (0.01)				

AIC, Akaike's information criterion; ΔAIC, AIC differences between models; w_i, Akaike weights; n, sample size.

off South Africa, Watson and Smale (1999) only used the second DFS, rejecting after several readings 12% of spines for age estimation; in contrast, in the present study only 8% of the spines used were rejected, probably as a result of the better readability of first DFS. Therefore, for *S. megalops*, the clearer pattern of bands observed in the first DFS made this structure easier to read and hence more suitable for age analyses than the second DFS.

The low values of the coefficient of variation (CV) and the average percentage error (APE) index for the within- and between-reader analyses suggested high precision for the age assessment of *S. megalops*. These two indices assume that variability among observations of individual fish can be averaged over all age classes, obscuring differences in precision (Hoenig *et al.* 1995). However, when calculations were made for each age class (within-reader only), between-age class variability was low. A trend of increasing within-reader precision was observed for the mid-range age classes, suggesting that these classes are easier to read. The age bias plot indicated no bias in the age estimation of Reader 1 (principal reader). Few studies on the age and growth of squalid sharks provide estimates of precision and bias, despite their importance for any ageing studies (Campana 2001). However, when such estimates are produced (Holden and Meadows 1962; Ketchen 1975; Nammack *et al.* 1985; Clarke *et al.* 2002*a*, 2002*b*; Irvine 2004), most studies report high reproducibility of age estimates, further supporting the use of spines as a precise approach for ageing squalid sharks.

Analysis of the enamel edge of whole spines supports the hypothesis of annual band formation in *S. megalops*. The peak in dark bands observed during late autumn-winter (May to July), followed by the peak in light bands during spring-early summer (October to December), and by the peak in wide light bands during early autumn (March to April), was the expected pattern for annual band deposition. A similar pattern was reported for *Squalus acanthias* off north and west Scotland (Holden and Meadows 1962) and off the north-eastern USA (Nammack *et al.* 1985). For *S. acanthias*, the timing of light and dark band formation on the enamel edge of spines was validated using mark-recapture oxytetracycline (OTC)-tagged sharks (Tucker 1985).

Band counts of the inner dentine layer (spine sections) of first DFS of *S. megalops* were in good agreement with counts of the enameled surface, verifying the age estimates obtained from counts of the enameled surface of spines. Counts of bands of the inner dentine have been used for age estimation of other squalid sharks (e.g. Clarke *et al.* 2002*a*, 2002*b*; Irvine 2004). For *S. acanthias*, comparisons of internal (sections) and external (enameled surface) counts agreed within ±2 bands (Holden and Meadows 1962). However, for the deepwater velvet dogfish *Centroscymnus crepidater*, Portuguese dogfish *C. coelolepis* and New Zealand lantern shark *Etmopterus baxteri*, the number of external bands exceeded the number of internal bands in sharks older than 3 to 5 years (Irvine 2004).

Several authors (e.g. Beamish and McFarlane 1983; Cailliet 1990; Campana 2001) have stressed the need for validation of the temporal periodicity of band deposition and of the absolute age for accurate age estimation. Captive rearing of OTC-tagged *S. megalops* was attempted in order to validate the periodicity of band deposition. However, as with a similar study in South Africa (Watson and Smale 1999), maintenance of sharks in captivity was met with limited success. More rigorous methods of age validation, such as the bomb radiocarbon method (Druffel and Linick 1978), is not applicable to *S. megalops* because samples of sharks born during the period of ^{14}C increase (1955 to 1970) are not available. Annual deposition of bands on spines of squalid sharks has been validated for *S. acanthias* on both sections and the enameled surface of whole spines (Beamish and McFarlane 1985; Tucker 1985; McFarlane and Beamish 1987). Although it does not necessarily follow that these bands are annual in other squalid sharks (Clarke *et al.* 2002*b*), for *S. megalops*, the most parsimonious interpretation of available evidence (edge analysis and comparisons of internal and external bands) points to annual formation of bands. However, further research

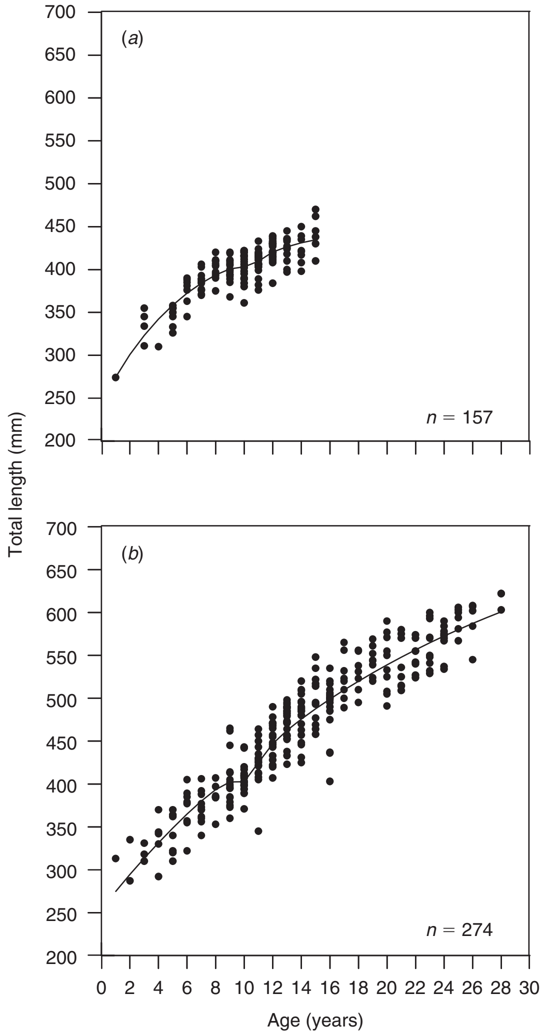

Fig. 7. Two-phase von Bertalanffy growth model (TPVBGM) fitted to length-at-age data derived from counts on the first dorsal fin spine (DFS) of (*a*) male and (*b*) female S*qualus megalops*. Estimates of model parameters are given in Table 4.

is needed to confirm annual band deposition and absolute age of *S. megalops*. A pilot tagging study gave promising results (9 recaptured sharks out of 617 tagged; Brown *et al.* 2000); hence, a large-scale release-recapture program of known-age and marked sharks or OTC-tagged sharks (Beamish and McFarlane 1985; Campana 2001) would provide information on periodicity of band deposition.

Growth model selection is not a straightforward process. Based on the goodness-of-fit criterion used (Akaike's Information Criterion, AIC), the best model for both sexes was the two-phase von Bertalanffy growth model (TPVBGM). The use of a TPVBM allows growth to be divided into two phases, such as changes in habitat (e.g. from coastal to off-shore waters), feeding habits (e.g. from a planktivorous to a piscivorous diet) or energy allocation (e.g. from energy allocated to growth, as in juveniles, to energy allocated to growth and reproduction, as in adults). For male *S. megalops* the change in growth rate corresponded with size at maturity, whereas for females, the change was slightly before the size females began to mature (Braccini *et al.* 2006*a*). This would support the energy allocation hypothesis as an explanation of two-phase growth. However, the other two hypotheses cannot be discarded, because *S. megalops* exhibits a strong pattern of size segregation (Graham 2005; Braccini *et al.* 2006*b*) where juveniles and adults may occur in different habitats, and large and small individuals have different feeding habits (Braccini *et al.* 2005).

The quality of data used in the fitting process and the shape of the growth curve are of similar importance in the description of the growth process, particularly when samples are collected from commercial fishing operations. When growth models are fitted to these types of data, the resulting parameters may be different from those obtained from a more representative sample (Haddon 2001). Most studies on age and growth of elasmobranchs obtain samples from commercial fisheries and assume that data are unbiased. However, the length-age scattergram and the growth curve of *S. megalops*, particularly of females (see Fig. 7 of the present study; Watson and Smale 1999), and other shark species (e.g. Moulton *et al.* 1992; Cannizzaro *et al.* 1995) does not asymptote, suggesting that either samples are not representative of the entire population and further sampling of large individuals is required, or that those species do not exhibit an asymptotic maximum length and hence asymptotic models are not adequate to describe growth. Linear growth of long-lived species such as sharks has only been reported for juveniles (e.g. Simpfendorfer 2000) or when sampling is not representative of all size classes (e.g. Wintner 2000). Hence, it is more likely that the observed scattergram and the subsequent growth curve derived are products of unrepresentative data, owing to a combination of several factors. Length-selective sampling bias and length-selective fishing mortality of gill-nets can cause distortions to growth curves (Moulton *et al.* 1992; Walker *et al.* 1998). In the present study, most samples were collected from demersal otter trawl and Danish seine vessels. Although the selectivity of the mesh of the trawl cod-end is not adequately understood, length-selective sampling bias and fishing mortality might partially account for the shape of the growth curve and the scatter of data points for *S. megalops*.

The movement pattern of *S. megalops* may affect the size classes encountered by the trawl fishery. Parturition is likely to occur outside the fishing grounds (Graham 2005). Because *S. megalops* is an opportunistic predator that consumes a wide range of prey items, larger neonates and juveniles are thought to move to the fishing areas to feed on trawl discards or prey exposed by trawl operations that disturb sediments (Braccini *et al.* 2005). Hence, the larger neonates and juveniles would then become available to sampling by the trawl gear and thereby create a bias in the size distribution of neonates and juveniles sampled, owing to a higher probability of collecting large, fast-growing individuals rather than small, slow-growing individuals. For intermediate-aged sharks, the large, fast-growing individuals of an age class may have been selectively removed from the population by fishing (Walker *et al.* 1998; Haddon 2001). This length-selective removal of the largest sharks of the available age classes by fishing has a biasing effect when sampling these age classes. Also, fishing mortality might have removed the older individuals from the population, making these age classes not available to sampling. Alternatively, due to the strong size segregation exhibited by *S. megalops* (Graham 2005; Braccini *et al.* 2006*b*), if certain size class or size classes (e.g. the largest females of each age class) occurred outside the trawling areas, only the smallest individuals would be available for sampling and the size-at-age frequency distribution of the age classes would be biased. The biasing factors listed above might have distorted the size-frequency distribution of males and females, which might have led to the two-phase growth pattern observed. Therefore, alternative growth models such as VBGM and Gompertz should also be considered when modelling the growth dynamics of *S. megalops*.

Precision estimates, the relationship between spine total length and TL, edge analysis, and agreement between counts on the inner dentine layer and the enameled surface support the use of the first DFS for the age estimation of *S. megalops*. Based on goodness-of-fit criterion, the best growth model for males and females was the TPVBGM. However, model selection cannot only be based on quality of statistical fit and, given that length-at-age data might not be representative of real growth, results should be interpreted with caution. Regardless of the model used, the growth rate of *S. megalops* (particularly of females) is very low, even within the range of growth rates reported for shark species (0.03 to 1.337 years^{-1}) (Cailliet and Goldman 2004). The reproductive output of this species is also low: litter size is at most four and the reproductive cycle is almost two years (Braccini *et al.* 2006*a*). These characteristics indicate that *S. megalops* has low biological productivity and is therefore at higher risk to the effects of fishing than species with greater biological productivity.

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Redescription of two species of wobbegongs (Chondrichthyes: Orectolobidae) with elevation of *Orectolobus halei* Whitley 1940 to species level

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Abstract

Two closely related species of the genus *Orectolobus* (Orectolobidae), *O. ornatus* (De Vis) and *O. halei* Whitley, are redescribed based on fresh material from temperate eastern Australia. Although described as a subspecies by Whitley (1940), *O. halei* was formerly synonymized with *O. ornatus* because of the lack of research material to assess their conspecificity. Due to its smaller size, *O. ornatus* was previously thought to be the juvenile form of the larger *O. halei*. *Orectolobus ornatus* occurs from Port Douglas, (Queensland) to Sydney (New South Wales) whereas *O. halei* occurs from Southport (Queensland) around the southern coast to Norwegian Bay (Western Australia). Both species are commercially targeted within the hook and line fishery off New South Wales. *Orectolobus ornatus* differs from *O. halei* in color pattern, a smaller adult size, fewer dermal lobes at the posterior preorbital group, lower vertebral and spiral valve counts, and the absence of supraorbital knob. Morphometrically, *O. ornatus* has a longer pelvic fin to anal fin interspace, smaller pectoral fins, smaller head dimensions, and relatively smaller claspers in mature specimens.

Key words: Orectolobidae, *Orectolobus ornatus*, *Orectolobus halei*, redescription, NSW

Introduction

Wobbegong sharks (family Orectolobidae Gill 1896) are bottom-dwelling sharks found in warm temperate to tropical continental waters of the western Pacific (Compagno 2001). They can be distinguished from all other sharks (except angel sharks, family Squatinidae) by their flattened and variegated bodies, and from all other elasmobranchs by possessing dermal lobes along the sides of the head. Wobbegongs also have a short, nearly terminal mouth in front of the eyes, nasoral grooves, circumnarial grooves and flaps, symphysial grooves, large spiracles and dorsolateral eyes (Compagno 2001).

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The family currently comprises seven valid species that are divided into three recognized genera: *Eucrossorhinus* consisting of *E. dasypogon* (Bleeker 1867); *Orectolobus* consisting of *O. japonicus* Regan 1906, *O. maculatus* (Bonnaterre 1788), *O. ornatus* (De Vis 1883), *O. wardi* Whitley 1939, and *O. hutchinsi* Last *et al.* 2006; and *Sutorectus* consisting of *S. tentaculatus* (Peters 1864). The systematics of the family is not fully resolved and two new species of wobbegongs from Western Australia have recently been identified (P. Last and J. Chidlow personal communication). Furthermore, new material from Indonesia (W. White personal communication), Borneo (Manjaji 2002) and the Philippines (Compagno *et al.* 2005) suggests that additional species exist in the Indo-West Pacific.

Two species, *O. ornatus* and *O. maculatus*, are thought to occur off temperate eastern Australia, but it has been suggested that other closely related species-level taxa may also be present. Whitley (1940) described the subspecies *O. ornatus halei*, from southern Australia and distinguished it from *O. ornatus ornatus* from northeastern waters by “differences in its color pattern and in the form of the tentacles around the head”. No further description was given by Whitley apart for the size of the holotype of 288.3 cm. Furthermore, some specimens of *O. ornatus* are mature at 70–80 cm total length (TL) which is considerably smaller than the normal size of maturity at about 175 cm TL (Last and Stevens, 1994; Chidlow, 2001). This discrepancy between ‘small’ and ‘large’ morphs of *O. ornatus* was observed by Last and Stevens (1994) but they could not resolve the alpha taxonomy because of the paucity of research material. The small morph has since been observed mating (S. Hartley 2004 personal communication), and small pregnant females are regularly caught in the targeted wobbegong commercial fishery (Huveneers unpublished data). Apart from these reports, there has been no positive evidence to support the existence of a third species off eastern and southern Australia. The original description of *O. ornatus halei* was inadequate and it has subsequently been considered as a synonym of *O. ornatus* (Compagno 2001).

Wobbegongs have been targeted off the eastern Australian state of New South Wales (NSW) by commercial fishers for at least 15 years. However, catches have declined over the past decade leading to public concern about the potential impact of the fishery on wobbegong populations (NSW Department of Primary Industries 2001). There are minimal management strategies specifically regulating wobbegong fisheries in NSW. Those currently in place directly applying to wobbegongs are a recreational bag limit of two wobbegongs per day, gear limit of no more than ten lines each with a maximum of six hooks when setlining within three nautical miles of the coast, and the *defacto* protection given to shared critical habitats with grey nurse shark (*Carcharias taurus*). The lack of specific strategies directed at wobbegong commercial fishing and the decline in catches, has resulted in *O. ornatus* and *O. maculatus* being listed as ‘Vulnerable’ in the IUCN Red List in NSW and as ‘Near Threatened’ globally (Cavanagh *et al.* 2003). NSW Department of Primary Industries (NSW DPI) has expressed the need for appropriate management to ensure the viability of wobbegong populations in NSW (NSW DPI 2001). Suitable regulations require knowledge of all wobbegongs species marketed in NSW, especially if the sizes at maturity and reproductive biology differ between those species. Consequently, the subspecies needed to be investigated to help distinguish them and assess their conspecificity. These taxa are shown to be non-conspecific and both taxa are fully described below. A taxonomic key to *Orectolobus* species in NSW is also provided.

Material and methods

Morphometrics followed Compagno (1984, 2001), with additional measurements taken to incorporate the different morphology of orectolobids. Dermal lobe measurements followed Last *et al.* (2006). Additionally, the distance between the nasal barbel and the anterior preorbital group (nasal-preorbital space), as well as the distance between the preorbital groups (preorbital space), were also measured. Several new head measurements were also measured to account for subtle differences in head morphology: head height at eye level (HDHe) (Fig. 1), head width at anterior of spiracle level (HDWs), head width at anterior of posterior preorbital lobes (HDWpo), and head width at nasal barbel level (HDWn) (Fig. 2). Caudal fin measurements varied from Compagno (2001) due to the difference in shape compared with carcharhinid sharks (Fig. 3). Counts and measurements for the holotype are given first, followed by ranges of all specimens examined. Meristics were taken from X-rays. Tooth row counts, which are difficult to obtain from radiographs, were taken directly from specimens. Spiral valve whorl counts were obtained from dissecting other specimens collected at the same locations as registered specimens.

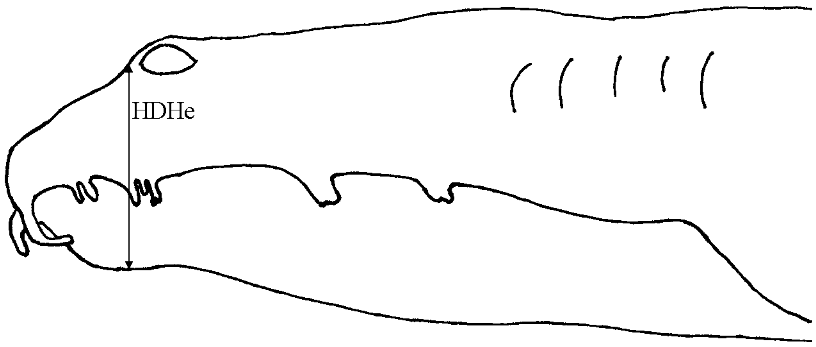

FIGURE 1. Lateral view of *Orectolobus ornatus* showing new head height measurement (HDHe: head height at eye level).

New material of the large morph were collected by NSW commercial fishers targeting wobbegongs using setlines off Sydney (34° 14S, 151° 04E). Specimens of the small morph were caught using a handnet (under NSW Fisheries permit number P03/0057) using SCUBA off Tomaree Head, Port Stephens (32° 43S, 152° 11E). The holotype of *O. ornatus* is held at the Queensland Museum (QM) and the newly designated neotype of

O. halei was deposited at the Australian Museum (AMS). Other new material was dispersed between the AMS and the Australian National Fish Collection (CSIRO). Additional specimens were examined at the AMS, CSIRO and QM. Other institutional abbreviations follow Leviton *et al.* (1985).

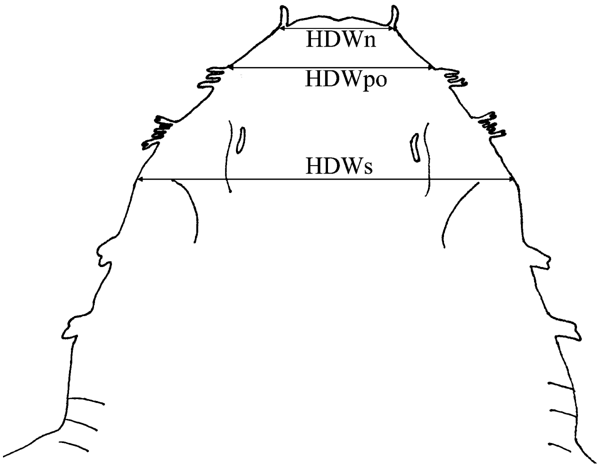

FIGURE 2. Dorsal view of *Orectolobus halei* showing new head width measurements (HDWs: head width at anterior of spiracle level; HDWpo: head width at anterior of posterior preorbital lobes level; HDWn: head width at nasal barbel level).

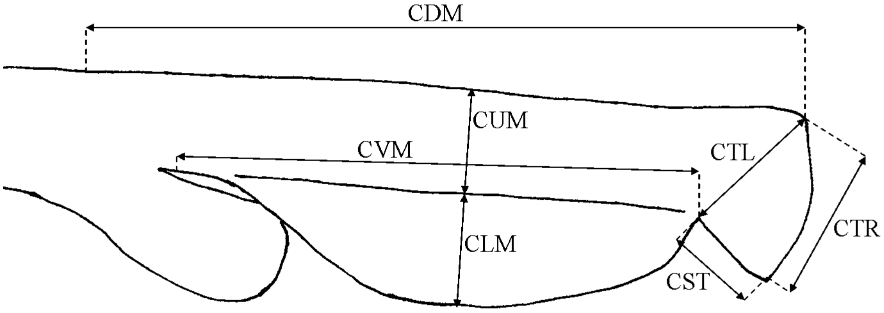

FIGURE 3. Lateral view of caudal fin showing measurements (CDM: dorsal caudal fin margin; CVM: ventral caudal fin margin; CUM: upper caudal fin margin; CLM: lower caudal fin margin; CTL: terminal caudal fin margin; CST: subterminal caudal fin margin; CTR: terminal caudal fin margin).

Results

Orectolobus halei Whitley, 1940

(Figs. 4–6, Table 1–2)

Material examined

Holotype. SAMA 2883 mm TL female (cast), type locality: St. Vincent Gulf, South

Australia. Lost according to Eschmeyer (CD-Rom, 1998).

Neotype (designated herein). AMS I 43628-002, 1700 mm TL, mature male, longline, type locality: the Hump, 3.3 nautical miles offshore between Garie Beach and Wollongong, 34° 14S, 151° 04E, 20–35 m, 9th June 2005, collector Charlie Huveneers and Jason Moyce.

Other specimens examined. AMS I43628-001, 1285 mm TL, female; CSIRO H 6278-01, 1775 mm TL, female; CSIRO H6278-02, 1869 mm TL, mature male; AMS I43628-003, 1520 mm TL, immature male. All four specimens collected using longline at the Hump, 3.3 nautical miles offshore between Garie Beach and Wollongong, 34° 14S, 151° 04E, 20–35 m, 9th June 2005, collector Charlie Huveneers and Jason Moyce. AMS I43629-001, 1140 mm TL, immature male, setline, Merimbula 50–100m from shore, 36° 54S, 149° 57E, 10–20 m, 24th April 2005, collector Charlie Huveneers, Shannon Corrigan and Shannon Fantham.

Diagnosis

A large species of *Orectolobus* with the following combination of characters: no warty tubercles on head or body; four groups of dermal lobes below and in front of eyes on each side of head; no dermal lobes on chin; nasal barbel closest to mouth branched; five to six lobes in second preorbital group (rarely four) with lobes at extremities usually longer and branched; broad branched postspiracular groups; two supraorbital knobs; base of anterior postspiracular lobe 3.28–3.69 in its distance from postorbital group, 1.36–2.36 in its distance from posterior postspiracular lobe; pelvic-fin insertion at first dorsal-fin midpoint; prepelvic length 2.40–3.13 times pelvic-anal space; pelvic-caudal space 1.04–1.25 times trunk width; teeth in upper jaw 25–28, those in medial row at symphysis rudimentary; spiral valve turns 29–32; precaudal vertebrae count 108–112. Light and dark brown coloration with nine darker brown, blotch-shaped saddles located dorsally; each saddle has conspicuous black edges.

Description

Body depressed anteriorly from snout to pelvic-fin origin, slightly firm dorsal musculature with relatively flaccid flanks; trunk depressed, broadest over midtrunk; body shape changing from depressed to compressed and tapering from pelvic-fin origin; dorsal musculature slightly elevated from flank musculature forming a small ridge from the fifth gill slit to pelvic-fin insertion, decreasing anteriorly to first dorsal-fin origin. Head broad, strongly depressed, somewhat oval in cross-section with truncate anterior when viewed from above, length 21.4 (21.0–21.8) % TL, 2.08 (2.08–2.76) times second dorsal-fin origin to anal-fin origin, height at gill level 8.5 (7.3–9.1) % TL, 1.74 (1.33–1.74) in pelvic-fin midpoint to first dorsal-fin insertion; trunk width 21.7 (20.4–23.0) % TL; abdomen elongate, width 5.94 (5.26–6.34) % TL. Pectoral-pelvic space 19.3 (16.8–21.9) % TL, 0.90 (0.73–1.00) times head length; pelvic-anal space 2.10 (1.93–2.50) times anal-fin base; snout-vent length 0.99 (0.99–1.04) times vent-caudal length. Caudal peduncle absent, lower origin of caudal fin almost connected to anal-fin insertion, strongly compressed, oval in cross section at anal-caudal junction, caudal peduncle width 1.59 (1.33–1.64) in height.

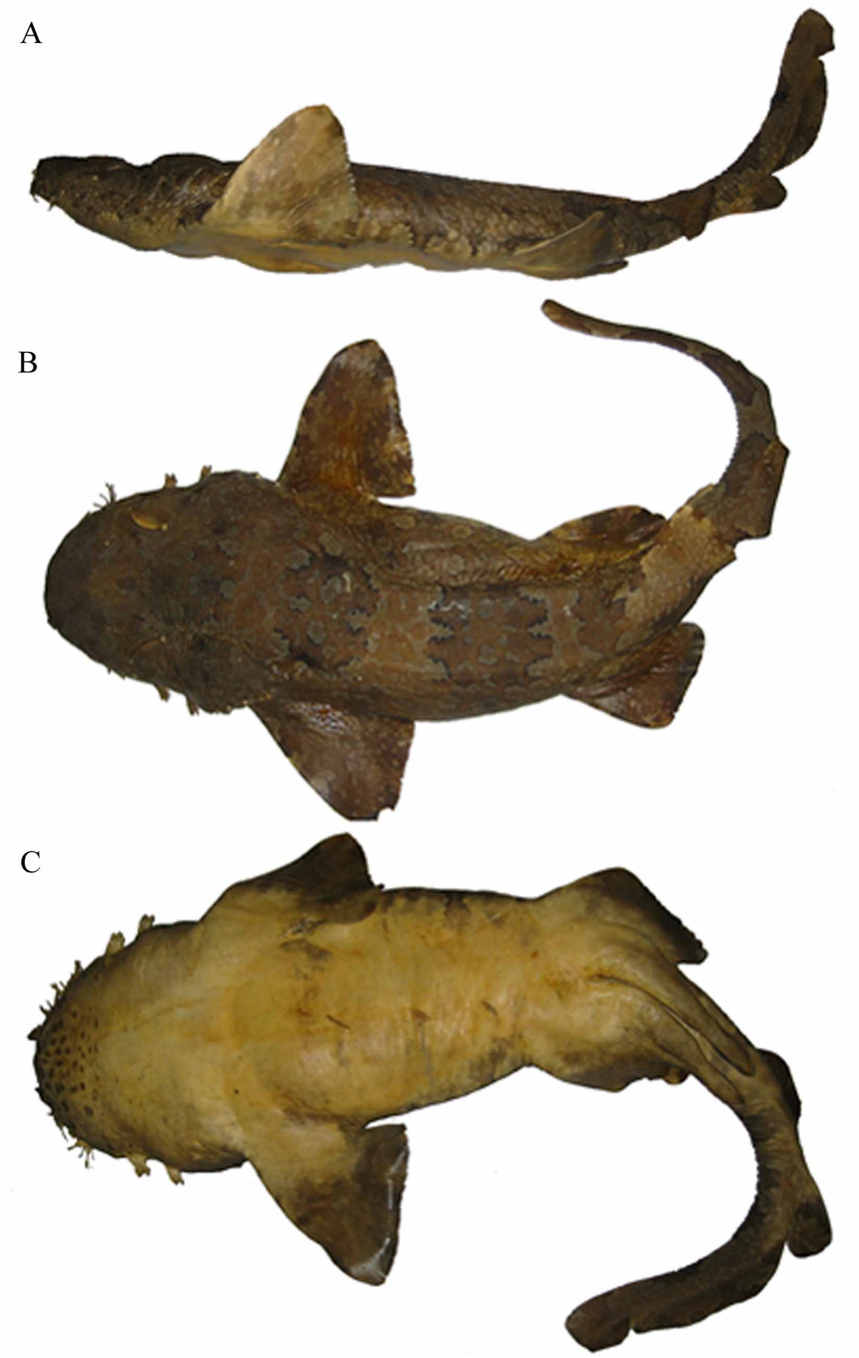

FIGURE 4. Photographs of neotype *Orectolobus halei* AMS I 43628-002, 1700 mm TL, mature male: A) lateral view; B) dorsal view; and C) ventral view.

Snout short, narrowly rounded in lateral view, truncate in dorsoventral view, slightly rounded angles; preoral length 0.8 (0.8–1.2) % TL, 12.50 (8.33–12.50) in mouth width; prenarial length negligible. Eyes dorsal on head, small, slit-like, length 1.7 (1.5–1.8) % TL, 12.35 (12.35–12.99) in head length; supraorbital crest elevated over and behind eye; two knobs on supraorbital crest, posterior knob longer; weak supraorbital ridge extending above spiracle; subocular pocket 2.26–2.70 times eye length; interorbit weakly concave. Spiracles slit-like, oblique to horizontal axis, longer than eye, 1.99 (1.91–2.29) times eye length; anterior margin convex well elevated above weakly convex posterior margin; small eye spiracle space 0.4 (0.3–0.6) % TL; fold above spiracle anterior margin. Gill slits lateral on head, first three of similar length (2.2–3.0 % TL), fourth gill slit smaller, 0.94 (0.82–1.01) times third gill slit, last gill slit longest 1.17 (1.00–1.27) times first; last gill slit anterior to pectoral-fin midbase; pectoral-fin origin between second and third gill slit. Mouth subterminal, large 3.1 (2.9–3.3) % TL, horizontally expanded, broadly arched, width 10.7 (9.6–10.7) % TL, 3.47 (2.96–3.47) times its length, 4.76 (4.76– 5.26) in vent to caudal length; 0.96 (0.83–1.09) times dorsal-fin midpoint to pelvic-fin origin; upper labial furrows 4.3 (4.1–4.9) % TL, originating at ventral margin of nostrils; lower labial furrows longer 5.4 (4.6– 5.5) % TL, almost connected near symphysis of lower jaw. Nostrils small, widely separated, internarial space 5.4 (4.5–5.4) % TL, adjacent upper lip of mouth. Nasal barbel terminal on head, medial to nostrils, proboscis-like, rounded basally, tapering distally, length less than upper labial furrows; short flattened branched lobe at basal third of posterior margin; lateral nasal lobe broad, well elevated, subcircular, most expanded posteriorly.

Fang-like teeth relatively large, long and pointed, not exposed when mouth closed. Upper jaw with rudimentary symphysial tooth recessible into upper lip and flanked distally by one larger symphysial on either side. Lower jaw with three rows of enlarged symphysials, their cusps subequal in length to each other and to those at symphysis in upper jaw; tooth cusps distal to symphysis decreasing sequentially in size; tooth shape varies distally from symphysis, first two to three teeth lack cusplets, one to two cusplets from the third or fourth parasymphysial on either side of the cusp on about four to seven teeth, distal cusplets more pronounced than medial ones, three to five most distal teeth generally lack cusplets on either side of cusp; teeth formula (n = 14): upper jaw (11–12) +1 + 1 + 1 + (11–12) = (25–27); lower jaw (8–11) + 3 + (8–10) = (19–24).

Dermal lobes well developed; anterior preorbital group with three to four simple lobes, posterior lobe longest; posterior preorbital group with five to six lobes, longest lobes at extremities, anterior and second most posterior lobe longer and branched; combined distance across preorbital groups 8.3 (7.0–9.8) % TL; anterior and posterior postspiracular group with short, broader, branched single lobe, base width of anterior postspiracular lobe 1.6 (0.9–1.7) % TL, base width of posterior postspiracular lobe 1.7 (0.8–1.7) % TL; distance between prorbital group and anterior postspiracular lobe 3.5 (3.2–4) % TL, between postspiracular lobes 1.9 (1.9–2.5) % TL.

Dermal denticles small, non-imbricated, crown shield-like, weakly tricuspidate at anterior end, weak ridge on all cusps at anterior end, rounded posterior end. Clasper elongate, extending well beyond tip of pelvic fins, inner length 17.8 (16.0–17.8) % TL, 6.40 (6.40–6.55) times width at base, tip bluntly pointed; four terminal cartilages: ventral terminal, accessory terminal cartilage (or spur), dorsal terminal 2 and dorsal terminal, approximate one-to-one ratio with all terminal cartilages, end-style of axial cartilage slightly calcified and fused with dorsal terminal. When terminal cartilages of clasper are open, spear-like extension near lateral side of axial 21.1 (18.5–24.7) % clasper shaft length.

Dorsal fins similar in size and shape, triangular; anterior margins oblique; apices broadly rounded, first dorsal-fin apex slightly more rounded than second dorsal-fin apex; posterior margins vertical, very slightly convex to straight; inner margin parallel originating at level of pelvic-fin rear tip; second dorsal-fin height 8.4 (7.6–9.3) % TL, 0.99 (0.69–0.99) times pelvic-fin midpoint to second dorsal-fin origin; pre-first dorsal-fin length 48.9 (48.1–50.1) % TL, pre-second dorsal-fin length 61.2 (61.2–64.7) % TL; first dorsal-fin origin forward of pelvic-fin insertion (3.5 % TL); second dorsal-fin insertion anterior to anal-fin origin (0.7–0.8 % TL).

Pectoral fin large, length 15.7 (13.4–15.7) % TL, 2.81 (2.81–3.01) times pelvic-fin inner margin length; base fleshy, anterior margin slightly convex; apex broadly rounded; posterior margin slightly convex; inner margin straight, free rear tip very broadly rounded; prepectoral length 16.2 (16.2–19.5) % TL; pectoral-pelvic space 19.3 (16.8–21.9) % TL.

Pelvic fins moderately large, length 14.9 (12.0–14.9) % TL; anterior margin straight; apex very broadly rounded; posterior margin convex; inner margin straight, free rear tip broadly rounded; origin slightly anterior to first dorsal-fin origin, insertion first dorsal-fin midpoint; prepelvic length 44.1 (44.1–46.4) % TL, 2.51 (2.40–2.68) times pelvic-anal space; pelvic-anal space 17.6 (17.1–18.7) % TL, pelvic-caudal space 22.8 (21.9–26.57) % TL, 1.05 (1.03–1.26) times trunk width.

Anal fin elongate**,** lobe-like, well developed, base 8.5 (7.5–8.9) % TL, 2.09 (1.55–2.20) times interdorsal space; anterior and inner margins almost parallel, anterior margin first slightly concave then slightly convex; apex very broadly rounded; posterior margin straight, much smaller than anterior margin; inner margin straight, free rear tip slightly rounded; origin slightly posterior to second dorsal-fin insertion, insertion slightly posterior to caudal-fin origin; anal-fin height 1.61 (1.45–1.85) in base length; second dorsal-fin origin to anal-fin origin 10.3 (8.2–10.3) % TL, second dorsal-fin insertion to anal-fin insertion 1.36 (1.11–1.48) times terminal caudal margin.

Caudal fin long, strongly compressed; dorsal caudal margin length 21.0 (19.1–21.6) % TL, its origin slightly anterior to anal-fin insertion; upper lobe originating as a very low ridge, slightly distinguishable; anterior margin with a deep inflexion near its origin; outer rim straight and oblique; rounded apices; terminal caudal lobe fan-like; terminal caudal margin 6.2 (5.5–6.2) % TL.

Vertebral counts (n = 7): pre-first dorsal count 54–55; pre-second dorsal count 78–80; precaudal count 108–112. Spiral valve whorl count: 29–32 (n = 32, based on discarded specimens).

Coloration

Body light and dark brown coloration with nine darker brown blotch-shaped saddles located dorsally; each saddle has conspicuous black edges followed by grayish coloration, light brown and gray freckle-like blotches between saddles; first saddle weakly visible, posterior to spiracle, anterior to second gill slit; second saddle at pectoral-fin base level, broader than long; posterior end of third saddle at pelvic-fin origin level, length similar to width, lighter brown saddle extending laterally; fourth saddle small, anterior to first dorsal -fin origin, overlapping with inflexion of first dorsal-fin; fifth saddle from first dorsal-fin midbase to slightly anterior to second dorsal-fin origin, extending laterally and ventrally below mid body, nearly connecting at ventral midline; sixth saddle from second dorsal-fin midbase to slightly anterior of caudal-fin origin, extending laterally and ventrally below mid body, nearly connecting at ventral midline; seventh saddle at origin of caudal fin, anterior to anal-fin insertion, longer than broad, extending laterally, not extending on lower lobe of caudal fin; eighth saddle on upper caudal lobe, longer than broad, extending laterally, not extending on lower lobe of caudal fin; ninth saddle slightly anterior to caudal -fin tip, extending laterally, not extending on lower lobe of caudal fin. Gray bluish blotches sometimes with black edges on saddles decreasing in number and size from fourth saddle. V-shaped pattern anterior to interorbit; white spot on posterior tip of spiracle.

Underneath of head, trunk, abdomen and snout uniformly pale yellow, mouth and labial furrows with dark brown spots extending between posterior dermal lobe preorbital groups. Tail with three darker brown stripes on the flanks.

Pectoral fins green brown with blotches, underneath yellow at base, increasing brown color towards posterior margins, slight light brown blotches and white freckles; pelvic fins brown gray with blotches, underneath yellow at base, increasing brown color towards posterior margins, slight light brown blotches and white freckles; anal fin green brown, similar to tail coloration; dorsal fins brown, darker brown where saddles occur, green gray blotches/spots; caudal fin green brown, darker brown where saddles occur.

Remarks

Orectolobus halei was previously synonymized with *O. ornatus* due to the similarity in morphology and color pattern. Whitley (1940) first mentioned this species as a subspecies of *O. ornatus* and only described it as differing from *O. ornatus* “in color pattern and the form of the tentacles around the head”. The holotype, lodged at the South Australian Museum, Adelaide (SAMA), has been missing since at least 1997. The designation of a neotype is required due to the following. First, the previous description was so incomplete as to make it impossible to reliably distinguish *O. ornatus* from *O. halei*. Secondly, there currently is a significant problem of misidentification between those two species within the targeted fishery for wobbegong sharks. Lastly, declining catches of wobbegong sharks strongly argue for a reliable means of identifying the target species.

Orectolobus halei can be distinguished from *O. ornatus* by several measurements (Table 1) and the two species also differ in 11 specific ratios (Table 2).

Orectolobus halei, which is regionally sympatric with *S. tentaculatus*, *O. maculatus*, *O. wardi*, *O. hutchinsi*, and two undescribed species of *Orectolobus* off WA, can be distinguished from these species by the combination of the number of dermal lobes, color pattern and the absence of tubercles. *Orectolobus hutchinsi* has slender unbranched postspiracular lobes (broad and branched in *O. halei* and *O. maculatus*) and a distinctive yellowish brown upper body coloration with well-defined, darker brown saddles containing paler markings that lacks whitish rings and blotches (unlike *O. ornatus* and *O. maculatus*) (Last *et al.*, 2006). *Sutorectus tentaculatus* has large rounded tubercles on both the head and body, not present in the adults of other members of the family Orectolobidae. *Orectolobus maculatus* has six to ten dermal lobes, *O. wardi* has unbranched nasal barbels, whereas *O. halei* has five dermal lobes and branched nasal barbels. *Orectolobus wardi* has a simple color pattern with fewer dark spots, while *O. maculatus* and *O. halei* have a more elaborate pattern of variegated spots and saddles. *Orectolobus maculatus* has white O-shaped spots and white blotches that are absent in *O. halei*.

TABLE 1. Morphometric data for the holotype of *Orectolobus ornatus* and neotype of *Orectolobus halei*, with ranges provided for the other specimens examined. Total length is provided in mm, measurements expressed as percentage of the total length. Measurements in bold highlights are those that appeared to differ between the two species (missing data is due to morphometric measurements being unmeasurable).

	O. ornatus				*O. halei*			
	Holotype	other specimens (n = 5)			Neotype	other specimens (n = 5)		
	QM I 164	Min	Max	Mean	AMS I 43628–002	Min	Max	Mean
Total length	560	876	925		1700	1140	1869	
Fork length	95.5	95.5	96.4	96.0	95.3	94.5	95.5	95.2
Partial length	60.4	60.0	62.8	61.3	60.2	59.3	62.0	60.4
Precaudal length	80.2	78.1	80.2	79.3	80.2	78.8	81.9	80.0
Prenarial length	2.5	2.4	2.8	2.5	2.9	2.6	2.9	2.8
Preoral length	1.5	0.9	1.5	1.1	0.8	0.8	1.2	0.9
Preorbital length	4.6	3.9	5.2	4.8	5.3	5.2	6.0	5.7
Prespiracular length	6.8	6.8	7.4	7.0	7.2	6.8	7.6	7.2
Prebranchial length	14.7	14.4	16.1	15.1	14.7	14.7	17.9	16.0

to be continued.

TABLE 1 (continued).

	O. ornatus				*O. halei*			
	Holotype	other specimens (n = 5)			Neotype	other specimens (n = 5)		
	QM I 164	Min	Max	Mean	AMS I 43628–002	Min	Max	Mean
Head length	**20.8**	**19.3**	**20.8**	**20.3**	**21.4**	**21.0**	**21.8**	**21.4**
Prepectoral length	17.3	15.3	19.1	17.5	16.2	16.2	19.5	18.0
Prepelvic length	**42.5**	**39.6**	**43.5**	**41.7**	**44.1**	**44.1**	**46.4**	**45.1**
Snout-vent length		**45.8**	**48.5**	**47.2**	**50.4**	**50.2**	**52.5**	**51.2**
Preanal length	74.3	71.8	77.4	74.4	72.6	71.9	74.7	73.1
Pre-first dorsal length	50.0	48.7	50.3	49.5	48.9	48.1	50.1	49.2
Pre-second dorsal length	64.5	61.6	64.5	63.1	61.2	61.2	64.7	63.1
Interdorsal space	5.2	3.6	5.2	4.3	4.1	4.1	4.9	4.4
Dorsal-caudal space	6.0	6.0	7.9	7.1	7.8	6.9	8.4	7.6
Pectoral-pelvic space	17.9	15.4	18.2	17.2	19.3	16.8	21.9	18.9
Pelvic-anal space	**23.0**	**19.6**	**23.0**	**21.5**	**17.6**	**17.1**	**18.8**	**18.0**
Pelvic-caudal space	**30.1**	**28.1**	**31.4**	**29.3**	**22.8**	**21.9**	**26.5**	**24.7**
Vent-caudal space		**53.0**	**56.1**	**54.6**	**50.7**	**49.3**	**50.9**	**50.4**
Eye length	1.7	1.6	2.0	1.8	1.6	1.5	1.8	1.6
Eye height	1.3	1.0	1.3	1.1	1.0	0.9	1.1	1.0
Interorbital space	6.7	6.2	6.8	6.5	5.4	5.4	6.8	6.4
Nostril width		0.5	0.7	0.6	0.7	0.6	0.8	0.7
Internarial space	4.4	4.4	5.1	4.8	5.4	4.5	5.4	5.0
Spiracle length	2.7	2.7	3.1	2.8	3.3	3.0	3.8	3.4
Eye-spiracle space	0.5	0.3	0.7	0.5	0.4	0.2	0.6	0.4
Mouth length	**2.6**	**2.4**	**2.6**	**2.5**	**3.1**	**2.9**	**3.3**	**3.1**
Mouth width	**8.6**	**8.6**	**9.1**	**8.9**	**10.7**	**9.6**	**10.7**	**10.1**
Upper labial furrow length	**3.9**	**3.6**	**4.0**	**3.9**	**4.3**	**4.1**	**4.9**	**4.3**
Lower labial furrow length	4.3	4.2	4.6	4.3	5.4	4.6	5.5	5.1
Intergill length	5.3	4.6	5.5	5.1	5.5	4.8	6.2	5.5
First gill-slit height	**1.6**	**1.6**	**2.1**	**1.8**	**2.8**	**2.2**	**2.8**	**2.6**
Second gill-slit height	**1.8**	**1.6**	**2.1**	**1.9**	**2.8**	**2.6**	**3.0**	**2.7**

to be continued.

TABLE 1 (continued).

	O. ornatus				*O. halei*			
	Holotype	other specimens (n = 5)			Neotype	other specimens (n = 5)		
	QM I 164	Min	Max	Mean	AMS I 43628–002	Min	Max	Mean
Third gill-slit height	**1.6**	**1.6**	**2.0**	**1.8**	**3.0**	**2.5**	**3.0**	**2.7**
Fourth gill-slit length	**1.6**	**1.5**	**1.8**	**1.7**	**2.8**	**1.9**	**2.8**	**2.4**
Fifth gill-slit	2.4	2.4	2.7	2.5	3.5	2.6	3.5	3.1
Head height at third gill level	8.9	7.9	8.9	8.3	8.5	7.3	9.1	8.4
Head height at eye level	6.1	5.0	6.1	5.5	6.9	5.1	6.9	6.0
Head width at third gill level	**16.8**	**16.8**	**18.5**	**17.7**	**22.0**	**19.5**	**22.0**	**20.6**
Head width at spiracle level	14.5	14.4	16.0	15.3	17.5	16.0	17.9	16.9
Head width at posterior preorbital lobes	10.7	10.7	12.6	11.8	10.7	8.7	10.7	9.5
Head width at nasal barbel	6.0	6.0	6.7	6.3	6.5	6.0	6.7	6.3
Trunk height	9.6	7.3	9.6	8.1	8.8	7.6	9.4	8.5
Trunk width	17.4	16.9	18.7	17.8	21.6	20.4	23.0	21.7
Abdomen height	6.1	5.0	6.1	5.5	5.2	4.8	6.0	5.4
Abdomen width	5.5	5.3	5.7	5.5	5.9	5.9	6.3	6.2
Tail height	8.4	7.5	8.4	7.8	7.6	6.0	7.9	7.0
Tail width	9.0	7.5	9.0	7.9	7.7	3.3	8.1	6.2
Caudal peduncle height	2.8	2.8	3.3	3.0	3.5	3.0	3.5	3.3
Caudal peduncle width	4.0	2.1	4.0	2.5	2.2	2.1	2.5	2.2
Girth	45.6	42.0	45.6	43.2	48.4	42.1	49.9	46.9
Pectoral-fin length	**12.7**	**12.2**	**13.6**	**13.0**	**15.7**	**14.1**	**15.7**	**14.7**
Pectoral-fin anterior margin		**12.7**	**13.6**	**13.1**	**17.9**	**15.1**	**17.9**	**16.5**
Pectoral-fin base	**7.8**	**6.9**	**8.2**	**7.8**	**9.5**	**8.5**	**10.2**	**9.7**
Pectoral-fin height		**10.0**	**11.8**	**10.8**	**14.8**	**12.0**	**14.8**	**13.8**
Pectoral-fin anterior margin	5.1	4.6	5.4	5.1	5.6	4.9	5.6	5.1

to be continued.

TABLE 1 (continued).

	O. ornatus				*O. halei*			
	Holotype	other specimens (n = 5)			Neotype	other specimens (n = 5)		
	QM I 164	Min	Max	Mean	AMS I 43628–002	Min	Max	Mean
Pectoral-fin posterior margin		**11.1**	**12.9**	**11.6**	**16.1**	**14.5**	**16.1**	**15.2**
Pelvic-fin length	11.0	11.0	14.5	13.0	14.9	12.0	14.9	13.5
Pelvic-fin anterior margin	9.5	7.9	10.2	9.1	10.5	8.2	10.9	9.9
Pelvic-fin base	8.1	8.1	11.8	10.4		9.7	12.5	10.5
Pelvic-fin height	5.4	5.4	7.5	6.3	7.1	7.1	8.7	7.9
Pelvic-fin inner margin	3.6	3.0	3.6	3.3	3.5	3.4	4.7	4.0
Pelvic-fin posterior margin	7.2	7.2	10.9	9.2	11.2	9.0	11.2	10.2
Outer clasper length (mature specimens)		**8.3**	**8.9**	**8.6**	**10.1**	**9.2**	**10.1**	**9.6**
Inner clasper length (mature specimens)		**14.6**	**15.6**	**15.2**	**17.8**	**16.0**	**17.8**	**16.9**
Clasper base (mature specimens)		**3.0**	**3.7**	**3.4**	**2.8**	**2.4**	**2.8**	**2.6**
First dorsal-fin length	12.8	12.6	13.9	13.3	13.6	12.4	13.9	13.1
First dorsal-fin anterior margin	11.4	11.4	12.7	12.1	13.9	11.7	13.9	12.7
First dorsal-fin base	9.3	9.3	10.7	10.2	10.4	8.9	10.9	10.0
First dorsal-fin height	6.4	6.4	8.4	7.8	9.2	7.6	9.2	8.3
First dorsal-fin inner margin	2.8	2.8	3.8	3.2	3.9	3.2	3.9	3.5
First dorsal-fin posterior margin	7.7	7.7	9.3	8.7	9.5	8.5	9.8	9.0
Second dorsal-fin length	12.2	12.0	12.9	12.5	13.1	11.8	13.1	12.2
Second dorsal-fin anterior margin	11.0	10.2	11.2	10.9	12.2	10.9	12.2	11.6
Second dorsal-fin base	10.0	9.4	10.4	9.8	10.2	8.9	10.2	9.4
Second dorsal-fin height	6.4	6.4	8.0	7.2	8.4	7.6	9.3	8.4

to be continued.

TABLE 1 (continued).

	O. ornatus				*O. halei*			
	Holotype	other specimens (n = 5)			Neotype	other specimens (n = 5)		
	QM I 164	Min	Max	Mean	AMS I 43628–002	Min	Max	Mean
Second dorsal-fin inner margin	2.7	2.6	3.5	3.0	3.1	2.9	3.5	3.2
Second dorsal fin posterior margin	7.4	7.4	8.9	8.3	8.9	8.1	9.8	9.0
Anal-fin length	8.9	8.9	11.3	10.0	10.7	9.2	10.9	10.0
Anal-fin anterior margin	8.9	8.9	10.4	9.8	11.2	8.9	11.6	10.2
Anal-fin base	7.1	7.1	8.6	7.8	8.5	7.5	8.9	8.1
Anal-fin height	3.1	3.1	4.9	4.0	5.3	4.1	5.3	4.8
Anal-fin inner margin	2.5	2.4	3.0	2.7	2.9	2.1	3.0	2.6
Anal-fin posterior margin	2.5	2.5	3.9	3.4	3.9	3.6	4.0	3.8
Dorsal caudal margin	21.1	20.3	21.9	21.3	21.0	19.1	21.6	20.5
Lower caudal margin	2.8	2.8	3.6	3.3	3.7	3.1	3.9	3.6
Ventral caudal margin	14.0	14.0	15.7	14.9	15.0	13.9	15.5	14.6
Upper caudal margin	2.6	2.6	3.4	3.1	3.4	3.1	3.7	3.4
Subterminal margin	3.5	2.9	3.8	3.2	3.0	2.6	3.4	3.0
Terminal caudal margin	**4.3**	**4.3**	**5.1**	**4.7**	**6.2**	**5.5**	**6.2**	**5.9**
Terminal caudal lobe	**4.8**	**4.2**	**5.0**	**4.7**	**6.0**	**5.4**	**6.2**	**5.8**
First dorsal midpoint-pectoral insertion	39.1	30.3	39.1	32.2	30.5	27.0	31.3	29.7
First dorsal midpoint-pelvic origin	**13.5**	**13.4**	**15.4**	**14.0**	**11.2**	**8.9**	**11.8**	**10.3**
Pelvic midpoint-first dorsal insertion	**11.6**	**7.9**	**11.6**	**9.2**	**4.9**	**4.9**	**6.8**	**5.8**
Pelvic midpoint-second dorsal origin	**15.0**	**13.1**	**15.0**	**14.0**	**8.5**	**8.5**	**11.7**	**10.2**
Second dorsal origin-anal origin	**11.6**	**11.6**	**12.4**	**11.9**	**10.3**	**8.2**	**10.3**	**9.1**
Second dorsal insertion-anal insertion	7.6	7.6	9.8	9.1	8.5	6.8	8.5	7.7

to be continued.

TABLE 1 (continued).

	O. ornatus				*O. halei*			
	Holotype	other specimens (n = 5)			Neotype	other specimens (n = 5)		
	QM I 164	Min	Max	Mean	AMS I 43628–002	Min	Max	Mean
Nasal-preorbital space	**0.6**	**0.6**	**0.9**	**0.7**	**1.1**	**1.0**	**1.6**	**1.3**
Preorbital space	0.9	0.6	1.0	0.8	1.0	1.0	1.3	1.2
Preorbital-postspiracular space	3.8	3.5	4.8	4.2	3.5	3.2	4.0	3.5
Postspiracular space	2.6	1.5	2.6	2.3	1.9	1.9	2.5	2.2
Nasal barbel width	0.7	0.6	0.7	0.7	0.7	0.6	0.7	0.7
Anterior preorbital	1.3	1.3	1.6	1.5	1.9	1.4	1.9	1.5
Posterior preorbital	2.2	2.2	2.7	2.4	2.7	2.2	3.3	2.8
Anterior postspiracular	1.1	1.1	1.3	1.2	1.6	0.9	1.7	1.3
Posterior postspiracular	0.9	0.9	1.2	1.0	1.7	0.8	1.7	1.1

Size

To at least 2060 mm TL; males mature at 1684-1819 mm TL, females mature at 1605-1871 mm TL (Huveneers unpublished data).

Distribution

Temperate Australia, from Southport (27° 06S, 153° 26E), Qld, to Norwegian Bay (22° 54S, 113° 59E), WA. Southern records to Flinders Island (40° 19S, 147° 48E), Bass Strait.

Orectolobus ornatus **De Vis, 1883**

(Figs. 7–9, Table 1–2)

Material examined

Holotype. QM I 164, 560 mm TL, female, type locality: Moreton Bay, registered 5th of December 1911.

Other specimens. Five specimens: AMS I 43621-001, 890 mm TL, mature male; AMS I 43628-002, 890 mm TL, mature male; AMS I 43628-003, 876 mm TL, mature male; AMS I 43628-004, 925 mm TL, mature male; AMS I 43628-005, 905 mm TL, mature male. All specimens caught together in 5–10 m of water, 10–15 m off northern tip of Tomaree Head, Port Stephens, NSW, 32° 43S, 152° 11E. Collector Charlie Huveneers, Rob Harcourt and Roger Laird on the 7th and 8th of May 2005.

FIGURE 5. Photographs of holotype *Crossorhinus ornatus*, QM I 164, 560 mm TL, female: A) lateral view; B) dorsal view; and C) ventral view.

Diagnosis

A small *Orectolobus* species with the following combination of characters: no warty tubercles on head or body; four groups of dermal lobes below and in front of the eyes on each side of head; no dermal lobes on chin; nasal barbel closest to mouth branched; three lobes at second preorbital group (rarely four) with first and last lobes branched and longer than middle one; broad unbranched postspiracular groups; lack of supraorbital knobs; base of anterior postspiracular lobe 2.19–3.56 in its distance from postorbital group, 1.19–2.11 in its distance from posterior postspiracular lobe; pelvic-fin insertion anterior to first dorsal-fin midpoint; prepelvic length 1.78–2.22 times pelvic-anal space; pelvic-caudal space 1.52–1.95 times trunk width; teeth in upper jaw 23–27, those in medial row at symphysis rudimentary; spiral valve turns 20–23; precaudal vertebrae count 98–104. Brownish, greenish and grayish coloration with eight darker brown blotch-shaped saddles located dorsally; small light brown, freckle-like blotches between saddles.

Description

Body depressed anteriorly from snout to first dorsal fin origin, firmness of body unknown as holotype is a dry mount but other examined specimens have slightly firm dorsal musculature with relatively flaccid flanks; trunk depressed, broadest over midtrunk; body shape changing from depressed to compressed and tapering from pelvic-fin midpoint; dorsal musculature slightly elevated from flank musculature forming a small ridge from the fifth gill slit to pelvic-fin insertion, decreasing anteriorly to first dorsal-fin origin. Head broad, strongly depressed, somewhat oval in cross-section with truncate anterior when viewed from above, length 20.8 (19.3–20.8) % TL, 1.79 (1.61–1.79) times second dorsal-fin origin to anal-fin origin, height at gill level 8.9 (7.9–8.9) % TL, 0.77 (0.77–1.06) in pelvic-fin midpoint to first dorsal-fin insertion; trunk width 17.4 (16.9–18.7) % TL; abdomen elongate, width 5.5 (5.3–5.7) % TL. Pectoral-pelvic space 18.0 (15.4–18.2) % TL, 0.86 (0.74–0.92) times head length; pelvic-anal space 3.24 (2.58–3.24) times anal-fin base; snout-vent length (0.81–0.91) times vent-caudal length. Caudal peduncle absent, lower origin of caudal fin almost connected to anal-fin insertion, strongly compressed, oval in cross section at anal-caudal junction, caudal peduncle width 0.71 (0.71–1.56) times height.

Snout short, narrowly rounded in lateral view, truncate in a semi-hexagonal shape in dorsoventral view; preoral length 1.5 (1.0–1.5) % TL, 5.88 (5.88–10.00) in mouth width; prenarial length negligible. Eyes dorsal on head, small, slit-like, length 1.7 (1.6–2.0) % TL, 12.5 (10.00–12.50) in head length; supraorbital crest elevated over and behind eye; no supraorbital knob; ridge extending supraorbital crest above spiracle terminating slightly behind spiracle, terminating above spiracle in other specimens examined; supraocular crest absent in holotype, moderate in size in other specimens examined; interorbit flat to weakly convex, 3.89 (3.07–4.04) times eye length. Spiracles slit-like, oblique to horizontal axis, longer than eye, 1.56 (1.43–1.76) times eye length; anterior margin convex well elevated above concave posterior margin; small eye spiracle space 0.5 (0.3–0.7) % TL; fold above spiracle absent. Gill slits lateral on head, first three of similar length (1.6–2.1 % TL), fourth gill slit smaller, 0.91 (0.82–0.92) times second gill slit, last gill slit longest, 1.38 (1.18–1.46) times second, last gill slit anterior to pectoral-fin midbase; pectoral-fin origin between second and third gill slit. Mouth subterminal, large 2.2 (2.2–2.6) % TL, horizontally expanded, broadly arched, width 8.1 (8.1–9.1) % TL, 3.35 (3.35–3.81) times its length, 1.59 (1.49–1.59) in dorsal-fin midpoint to pelvic-fin origin; upper labial furrows 3.9 (3.6–4.0) % TL originating at ventral margin of nostrils; lower labial furrows longer 4.8 (4.2–4.6) % TL, 1.09 (1.07–1.17) times upper labial furrows, almost connected to symphysis of lower jaw. Nostrils small, widely separated, internarial space 4.4 (4.4–5.1) % TL, adjacent upper lip of mouth. Nasal barbel terminal on head, medial to nostrils, proboscis-like, rounded basally, tapering distally, length subequal to upper labial furrows; short flattened unbranched lobe at basal third of posterior margin; lateral nasal lobe broad well elevated, subcircular, most expanded posteriorly.

Fang-like teeth relatively large, long and pointed, not exposed when mouth closed. Upper jaw with rudimentary symphysial tooth recessible into upper lip and flanked distally by one larger symphysial on either side. Lower jaw with three rows of enlarged symphysials, their cusps subequal in length to each other and to those at symphysis in upper jaw; tooth cusps distal to symphysis decreasing sequentially in size; tooth shape varies distally from symphysis, first two to three teeth lack cusplets, one to two cusplets from the third or fourth parasymphysial on either side of the cusp on about four to seven teeth, distal cusplets more pronounced than medial ones, three to five most distal teeth generally lack cusplets on either side of cusp; teeth formula (n = 12): upper jaw (10–12) +1

+ 1 + 1 + (10–12) = (23–27); lower jaw (7–9) + 3 + (7–9) = (18–21).

Dermal lobes well developed; anterior preorbital group with two to three simple lobes, posterior lobe longest; posterior preorbital group with three lobes, anterior and posterior lobe longer and branched; combined distance across preorbital groups 6.7 (6.1–7.9) % TL; anterior and posterior postspiracular group with short, broader, unbranched single lobe, base width of anterior postspiracular lobe 1.1 (1.1–1.3) % TL, base width of posterior postspiracular lobe 0.9 (0.9–1.2) % TL; distance between prorbital group and anterior postspiracular lobe 3.8 (3.5–4.8) % TL, between postspiracular lobes 2.6 (1.5–2.6) % TL.

Dermal denticles small, non-imbricated, crown shield-like, weakly tricuspidate at anterior end, weak ridge on all cusps at anterior end, rounded posterior end. Clasper elongate, extending well beyond tip of pelvic fins, inner length of mature male 14.6–15.6 % TL, (3.91–5.06) times width at base, tip bluntly pointed; four terminal cartilages: ventral terminal, accessory terminal cartilage (or spur), dorsal terminal 2 and dorsal terminal, approximate one-to-one ratio with all terminal cartilages, end-style of axial cartilage slightly calcified and fused with dorsal terminal. When terminal cartilage of clasper is open, spear-like extension near lateral side of axial 16.9 (14.5–19.5) % clasper shaft length.

Dorsal fins similar in size and shape, triangular; anterior margins oblique; apices broadly rounded; posterior margins vertical, very slightly convex to straight; inner margin parallel originating behind pelvic-fin rear tip; second dorsal-fin height 6.3 (6.3–8.0) % TL, 0.43 (0.43–0.59) times pelvic-fin midpoint to second dorsal-fin origin; pre-first dorsal fin 50.0 (48.7–50.3) % TL, pre-second dorsal fin 64.5 (61.6–64.5) % TL; first dorsal-fin origin slightly forward to pelvic-fin insertion (1.6 % TL); second dorsal-fin insertion slightly anterior to anal-fin origin 1.9 (1.8–3.0) % TL.

Pectoral fin large, length 12.7 (12.2–13.6) % TL, 2.48 (2.40–2.74) times pelvic-fin inner margin length; unknown fleshiness of base due to preservation but fleshy base in other specimens examined; anterior margin slightly convex; apex broadly rounded; posterior margin slightly convex; inner margin straight, free rear tip very broadly rounded; prepectoral length 17.3 (15.3–19.1) % TL; pectoral-pelvic space 17.9 (15.4–18.2) % TL.

Pelvic fins moderately large, length 11.0 (11.0–14.5) % TL; anterior margin straight; apex very broadly rounded; posterior margin convex; inner margin straight, free rear tip broadly rounded; origin anterior to first dorsal-fin origin, insertion anterior to first dorsal-fin midpoint; prepelvic length 42.5 (39.6–43.5) % TL, 1.85 (1.83–2.22) times pelvic-anal space; pelvic-anal space 23.8 (19.6–23.8) % TL, pelvic-caudal space 30.1 (28.1–31.4) % TL, 1.73 (1.52–1.85) times trunk width.

Anal fin elongate, lobe-like, well developed, base 7.1 (7.2–8.6) % TL, 1.37 (1.37–2.15) times interdorsal space; anterior and inner margins almost parallel, anterior margin first slightly concave then slightly convex; apex very broadly rounded; posterior margin straight, much smaller than anterior margin; inner margin straight, free rear tip slightly rounded; origin slightly posterior to second dorsal-fin insertion; anal-fin height

2.27 (1.49–2.44) times base length; second dorsal-fin origin to anal-fin origin 11.1 (11.6–12.4) % TL; second dorsal-fin insertion to anal-fin insertion 1.74 (1.74–2.04) times terminal caudal margin.

Caudal fin long, strongly compressed; dorsal caudal margin length 21.2 (20.3–21.9) % TL. its origin slightly anterior to anal-fin insertion; upper lobe originating as a very low ridge, slightly distinguishable, anterior margin with a deep inflexion near its origin; outer rim straight and oblique; rounded apices; terminal caudal lobe fan-like; terminal caudal margin 4.1 (4.1–5.1) % TL.

Vertebral counts (n = 10): pre-first dorsal count 46–51; pre-second dorsal count 69–74; precaudal count 98–104. Spiral valve whorl count: 20–23 (n = 22, based on discarded specimens).

Coloration

Body brownish, greenish, and grayish with eight darker brown, blotch-shaped saddles located dorsally; light brown freckle-like blotches between saddles; first saddle broader than long, posterior to spiracle, anterior to first gill slit, symmetrical from dorsal midline; second saddle at pectoral-fin base level, broader than long; posterior end of third saddle at pelvic-fin origin level, length similar to width, lighter brown green saddle extending laterally; fourth saddle small, lighter brown, anterior to first dorsal-fin origin, overlapping with inflexion of first dorsal fin; fifth saddle from first dorsal-fin midbase to slightly anterior to second dorsal-fin origin, extending laterally and ventrally below mid body, nearly connecting at ventral midline; sixth saddle from second dorsal-fin midbase to slightly anterior to caudal-fin origin, extending laterally and ventrally, nearly connecting at ventral midline; seventh saddle at origin of caudal fin, anterior to anal-fin insertion, longer than broad, extending laterally, not extending on lower lobe of caudal fin; eighth saddle on upper caudal lobe, longer than broad, extending laterally, not extending on lower lobe of caudal fin; green gray blotches on saddles decreasing in number and size from snout to caudal fin. V-shaped pattern anterior to interorbit; white spot on posterior tip of spiracle.

Underneath of head, trunk and abdomen uniformly yellow green. Tail with three darker brown stripes on the flanks.

Pectoral fins light and dark brown with blotches and white freckles, underneath uniform yellow with white spots; pelvic fins light and dark brown with blotches and white freckles, underneath yellow at base, increasing brown green color towards posterior margins, slight blotches; anal fin gray brown, similar to tail coloration; dorsal fins light and dark brown with blotches and white freckles and darker brown where saddles occur; caudal fin brown green, darker brown where saddles occur.

Remarks

Orectolobus ornatus was previously considered to be juvenile *O. halei* due to its similarity in morphology and color pattern. It can be distinguished from *O. halei* by several measurements (Table 1) and also differs in 11 specific ratios (Table 2).

Orectolobus ornatus is also sympatric with *O. maculatus* and *O. wardi* and can be easily distinguished from them by the number of supraorbital knobs and dermal lobes, and the color pattern. *Orectolobus maculatus* and *O. wardi* have one or two supraocular knobs, whereas these knobs are absent in *O. ornatus* (Goto 2001). *Orectolobus maculatus* has six to ten dermal lobes, *O. wardi* has unbranched nasal barbels, whereas *O. ornatus* has five dermal lobes and branched nasal barbels. *Orectolobus wardi* has a simple color pattern with few dark spots while *O. maculatus* and *O. ornatus* have more elaborate variegated spots and saddles. *Orectolobus maculatus* has white rings that are absent in *O. ornatus*.

TABLE 2. Ranges of measurement ratios that appear to differ between *Orectolobus ornatus* and *Orectolobus halei*.

Ratios of morphometric measurements	*O. ornatus*	*O. halei*
Head length/second dorsal origin-anal origin	1.61–1.79	2.08–2.76
Prepelvic length/pelvic-anal space	1.83–2.22	2.40–2.68
Snout-vent length/vent-caudal length	0.81–0.91	0.99–1.04
Pelvic-caudal space/trunk width	1.52–1.85	1.04–1.26
Mouth width/first dorsal midpoint-pelvic origin	0.58–0.67	0.83–1.09
Head height at gill level/pelvic midpoint-first dorsal insertion	0.82–1.06	1.37–1.74
Pectoral length/pectoral inner margin	2.40–2.74	2.81–3.01
Second dorsal height/pelvic midpoint-second dorsal origin	0.43–0.59	0.69–0.99
Second dorsal insertion-anal insertion/terminal caudal fin margin	1.74–2.04	1.10–1.47
Preorbital-postspiracular space/lower labial furrow length	0.83–1.13	0.64–0.74
Spiracle length/eye length	1.43–1.76	1.91–2.29

Size

To at least 1017 mm TL; males mature between 796–830 mm TL, females mature between 795–864 mm TL (Huveneers 2005 unpublished data).

Distribution

Eastern Australia from Port Douglas (16° 32S, 145° 29E), Qld, to Sydney (151° 23E, 33° 36S), NSW.

Discussion

The very poor description of *O. halei* (Whitley, 1940) makes it impossible to quantitatively compare diagnostic features between the neotype herein designated and the previous description. The neotype was therefore assigned from the differing characters in "the color pattern and the form of the tentacles" as highlighted by Whitley (1940).

The aim of this paper was to define and redescribe *O. halei* and *O. ornatus* to facilitate species identification. Unfortunately, juvenile *O. halei* (smaller than 1100 mm) were not collected despite intensive searching over two years. The ranges of sizes of *O. ornatus* and *O. halei* examined did not overlap and thus differences in morphometry should be interpreted with caution due to allometric factors. Juvenile *O. halei* (smaller than 900 mm) are needed to confirm morphometric differences identified in this study.

The two species can, however, be differentiated using counts of precaudal vertebrae (greater than 105 in *O. halei* and less than 105 in *O. ornatus*) and/or spiral valves (greater than 26 in *O. halei* and less than 26 in *O. ornatus*). However, these characters are impractical for application in the field. Therefore, simpler but equally robust methods are needed to differentiate species under field conditions.

Total length is the simplest field character for differentiating NSW species. Any wobbegong exceeding 110 cm is either *O. halei* or *O. maculatus* (but not *O. ornatus*) and these two can be easily differentiated using color pattern and dermal lobes. Wobbegongs smaller than 110 cm are harder to identify. In the case of small males, if the claspers are calcified, the species is *O. ornatus*. For immature males or females, other traits have to be used. Color pattern may help identification with *O. ornatus*, which is freckled and green/gray (browner in *O. halei*), and lacks black edges along its saddle markings (otherwise present). However, coloration is highly variable in these species and *O. ornatus* specimens have been observed with an *halei*-like color pattern. Care must therefore be taken when using coloration alone to identify *Orectolobus* species.

Three further key features to differentiate between the two species are the number of dermal lobes at the posterior preorbital group, the position of the pelvic fins, and the supraorbital knobs. *Orectolobus ornatus* usually has only three lobes at the posterior preorbital group, consisting of two branched lobes at the extremities and a shorter unbranched lobe in the middle (more lobes are present in *O. halei*). However, both *O. ornatus* and *O. halei* have been observed with four lobes. Pelvic fins are located further back on *O. halei* with the pelvic-fin insertion at the level of the first dorsal midpoint (*O. ornatus* has the pelvic-fin insertion anterior to the first dorsal midpoint). Lastly, *O. halei* has two small knobs on the supraorbit (absent in *O. ornatus*).

By preference, these features should always be used together to maximize correct identification of *Orectolobus* species in NSW. Commercial fishers using these features should be able to identify *Orectolobus* species and report them accordingly. In the past, all species have been combined together as 'carpet shark'. Commencing in 2005, NSW DPI has required fishers to report *O. maculatus* separately. Using the characteristics described above, fishers should now be able to report catches of *O. maculatus*, *O. ornatus* and *O. halei* separately. Catch rate statistics could then be used to assess each species independently to investigate potential population decline.

Key to *Orectolobus* species in New South Wales

1. About 6 to 10 dermal lobes at the posterior preorbital group; white O-shaped spots and white blotches.. *Orectolobus maculatus*
About 3 to 6 dermal lobes at the posterior preorbital group; back with dark color variegated with blotches and prominent saddle markings 2

2. Spiral valve whorl count 20–23; precaudal vertebrae count 98–104; size-at-maturity about 800 mm; about 3 to 4 dermal lobes at the posterior preorbital group; no supraocular knobs; pelvic-fin insertion slightly anterior to the first dorsal midpoint .... *Orectolobus ornatus*
Spiral valve whorl count 29–32; precaudal vertebrae count 106–112; size-at-maturity about 1750 mm; about 4 to 6 dermal lobes at the posterior preorbital group; two distinct supraocular knobs; pelvic-fin insertion at about the level of the first dorsal midpoint... *Orectolobus halei*

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Morphometric Relationships and Catch Composition of Wobbegong Sharks (Chondrichthyes: *Orectolobus*) Commercially Fished in New South Wales, Australia

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Wobbegongs (Orectolobiformes) are commercially targeted in New South Wales, Australia. Catches have declined approximately 60% in a decade, leading to concerns over the fishery's sustainability. However, length and weight composition of the catch is unknown as carcasses are trunked (i.e. beheaded and eviscerated) before landing. We provide parameters for length–length, weight–weight and weight–length relationships to convert carcass length and carcass weight measurements to total lengths and total weights used in fisheries assessments. Neonates and small juveniles were conspicuously absent in the length-frequency distributions of all three species, suggesting the potential existence of nursery areas not available to the commercial fishery.

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KEYWORDS: commercial fishery, morphometric relationship, *Orectolobus*, wobbegong.

INTRODUCTION

Three species of wobbegong shark: the spotted wobbegong, *Orectolobus maculatus*, the dwarf ornate wobbegong, *O. ornatus*, and the large ornate wobbegong, *O. halei* (Huveneers 2006) occur in coastal waters off New South Wales (NSW), Australia and are commercially targeted by the Ocean Trap and Line fishery. Wobbegongs have been sold as 'boneless fillets' or 'flake' and their catch has declined from ~150 tonnes in 1990/91 to ~70 tonnes in 1999/00, a decrease of > 50% in less than a decade (Pease and Grinberg 1995; NSW Department of Primary Industries, unpublished data). This decline led to wobbegongs being listed as 'Vulnerable' (in NSW) and 'Near Threatened' (globally) under the World Conservation Union (IUCN) Red List assessment (Cavanagh et al. 2003) and to concerns over the sustainability of the fishery.

Given that many shark species, including wobbegongs, are trunked prior to landing, partial length and carcass weight are usually the only measurements that can be recorded (FAO 2000). Relationships between partial length and carcass weight and their respective total length and total weight are a fundamental requirement for an assessment of the catch composition, and towards the ecologically sustainable management of the fishery.

This study presents length–length, weight–weight, and weight–length relationships for each of the three species caught in the NSW commercial fishery. Catch composition and length-frequency distributions recorded during the study are also presented.

MATERIALS AND METHODS

Wobbegongs were collected from commercial fishers at six locations in NSW (Nambucca Heads, Port Stephens, Newcastle, Terrigal, Sydney and Eden) (Fig. 1). Wobbegongs were caught on setlines with O'Shaughnessy style hooks size 10/O or 12/O, with a 50–100 cm long wire or nylon trace attached to the bottom line by a stainless sharkclip. Hooks were baited with black fish (*Girella tricuspidata*), mullet (*Mugil cephalus*) or Australian salmon (*Arripis trutta*). Lines were set before sunset and hauled at

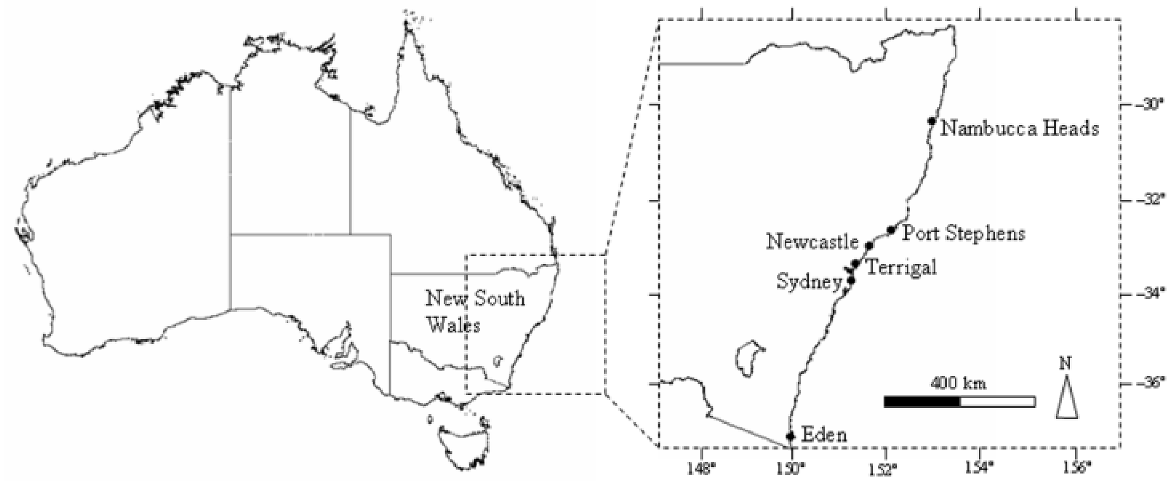

Figure 1. Sampling locations for collection of wobbegongs in New South Wales, Australia

sunrise on the following day.

The species, gender and a series of length measurements were recorded (to the nearest mm) for each shark caught. The length measurements included: total length (TL), snout to anal-fin insertion length (SAL), and partial length from the pectoral-fin origin to the caudal-fin origin (PL). SAL was taken instead of fork length as upper and lower caudal fin lobes of wobbegongs are not discernible. Total weight (TW) and carcass weight (CW) were recorded using spring balances (scale: 100 ± 0.2 kg, 20 ± 0.2 kg, 5 ± 0.1 kg).

Linear regressions of TL on SAL, TL on PL, and TW on CW were determined for each of the three species using data pooled across all sites. Log-transformed data were used for the regressions of TW on TL and CW on PL and corrected for biases caused by natural logarithmic transformation (Beauchamp and Olson 1973). Analyses of covariance (ANCOVA) were used to test for differences between sexes in all regressions. When the slopes and intercepts did not differ significantly between sexes the data were pooled and a common regression determined.

RESULTS

A total of 904 wobbegongs (435 males and 469 females) was collected comprising: 183 male and 202 female *O. ornatus* (combined range 471-1,017 mm TL), 97 male and 88 female *O. maculatus*, (combined range 870-1,575 mm TL), and 155 male and 179 female 334 *O. halei* (combined range 869-2,065 mm TL). Most *O. ornatus* (86.5%) were collected off Nambucca Heads with none caught south of Port Stephens. *Orectolobus maculatus* catches were distributed among Nambucca Heads (26.5%), Port Stephens (30.8%) and Sydney (37.8%), with none caught in Eden. *Orectolobus halei* were caught at all locations, with the majority caught off Sydney (62.6%), and sporadic captures at the remaining locations (Table 1). Neonates (born at ~21 cm for *O. ornatus* and *O. maculatus* and ~30 cm for *O. halei*) and small juveniles were absent in the catches of all three species (Fig. 2).

The conversion parameters estimated are applicable to the size range analysed (Table 1) which covers most of the population size range, with the exceptions of neonates and small juveniles (not caught by the commercial fishery). All regressions were significant with 19 correlation coefficients out of 22 over 0.84 (Table 2 and 3).

The slopes of the regressions of TL on SAL (Table 2) did not differ significantly between the sexes for *O. ornatus* and *O. maculatus* (ANCOVA: $F_{slopes} = 2.17$ and 0.62 respectively, $P > 0.05$), but the intercepts differed significantly between males and females (ANCOVA: $F_{intercepts} = 5.29$ and 11.06 respectively, both $P < 0.05$). The adjusted means showed that male *O. ornatus* and *O. maculatus* had a significantly greater TL for a given SAL compared to females. Similarly, the slopes of the regressions of TL on PL (Table 2) did not differ significantly between the males and females of *O. ornatus* and *O. maculatus* (ANCOVA: $F_{slopes} = 3.06$ and 0.17 respectively, $P > 0.05$). Again, the intercepts of the regressions of TL on PL (Table 2) differed significantly between the sexes (ANCOVA: $F_{intercepts} =$ 9.24 and 2.44, $P < 0.001$ and $P < 0.05$, respectively). The adjusted means showed that the male *O. ornatus* and *O. maculatus* had a significantly greater TL for

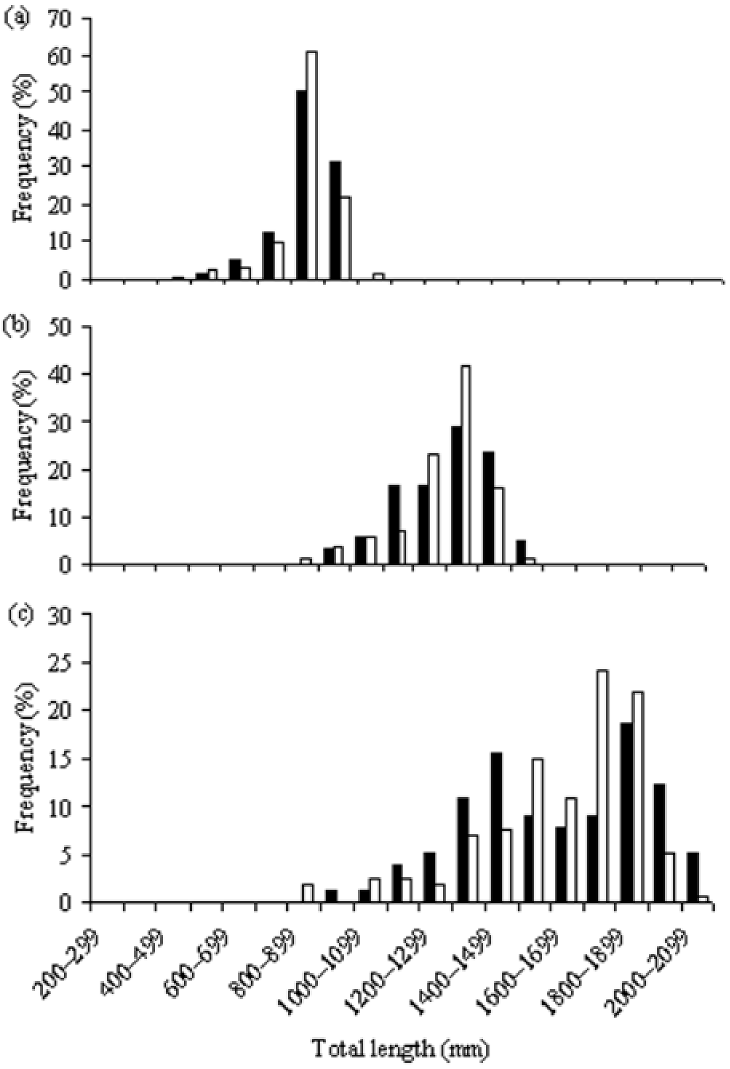

Figure 2. Length-frequency distribution of wobbegongs caught during sampling period for (a) *O. ornatus*, (b) *O. maculatus*, and (c) *O. halei* for males (solid bar) and females (open bar).

a given PL when compared to females. Neither the slopes nor intercepts of the regressions of TL on SAL and TL on PL (Table 2) differed significantly between the sexes for *O. halei* (ANCOVA: TL on SAL: F_{slopes} = 2.18 and $F_{intercepts}$ = 1.57, both $P > 0.05$; TL on PL: F_{slopes} = 0.31 and $F_{intercepts}$ = 0.40, both $P > 0.05$).

The slopes of the regressions of TW on TL (Fig. 3 and Table 3) differed significantly between male and female *O. ornatus* (ANCOVA: F_{slopes} = 6.62, $P < 0.05$) with weight increasing at a faster rate than in females. In contrast, slopes of the regressions of TW on TL (Table 3) for male and female *O. maculatus* and *O. halei* did not differ significantly (ANCOVA: F_{slopes} = 0.32 and 0.04 respectively, both $P > 0.05$), but the intercepts were significantly different between the sexes (ANCOVA: $F_{intercepts}$ = 20.20 and 5.49, $P < 0.001$ and $P < 0.05$, respectively). The adjusted means showed that females of *O. maculatus* and *O. halei* had a significantly greater TW for a given TL when compared to males.

Neither the slopes nor intercepts of the regressions of CW on PL (Table 3) differed significantly between the sexes for *O. ornatus*, *O. maculatus* and *O. halei* (ANCOVA: F_{slopes} = 1.95, 2.15 and 1.15; $F_{intercepts}$ = 0.01, 0.04 and 0.60; all $P > 0.05$ for *O. ornatus*, *O. maculatus* and *O. halei* , respectively).

DISCUSSION

The spatial distribution of wobbegong catches provides an indication of their distribution within NSW waters. Port Stephens was the southern-most location where *O. ornatus* was caught. Although *O. ornatus* have been recorded as far south as Sydney (207 km south of Port Stephens), no *O. ornatus* was caught around Sydney. Museum registered specimens have been collected as far north as the Whitsunday Islands (20° 20′S 148° 54′E, Australian Museum specimen IA 3831), restricting the distribution of *O. ornatus* from tropical to warm temperate waters of eastern Australia. *Orectolobus maculatus* is abundant in central NSW, around Port Stephens and Sydney. *Orectolobus maculatus* is caught in larger numbers in northern NSW than *O. halei* and has been recorded as far north as Gladstone (Kyne et al. 2005). In contrast to *O. halei*, *O. maculatus* was rarely caught around Merimbula and Eden (S. Fantham, pers comm.), restricting its distribution in eastern Australia from tropical to temperate waters. *Orectolobus halei* catches were low in northern NSW and higher around Sydney and Eden, where it was the only species caught during this study. In NSW, *O. halei* is more abundant in temperate waters with abundance decreasing in warm temperate waters. There is apparently a similar trend for *O. halei* collected in Western Australia (WA) (J. Chidlow, pers comm.).

Table 1. Number (with TL size range in mm) of wobbegong caught during June 2003–May 2006

Location	*O. ornatus*	*O. maculatus*	*O. halei*	Total
Nambucca Heads	333 (471–994)	49 (1,160–1,485)	31 (1,175–1,972)	411
Port Stephens	52 (577–1,017)	57 (870–1,440)	10 (1,280–1,875)	119
Newcastle		7 (1,265–1,435)	3 (1,444–1,755)	10
Terrigal		2 (unknown)	8 (1,860–1,930)	10
Sydney		70 (1,055–1,575)	209 (869–2,065)	278
Eden			73 (1,190–1,870)	64
Total	385 (471–1,017)	185 (870–1,575)	334 (869–2,065)	904

Table 2. Relationships between length–length and weight–weight. Estimated parameters (and standard error) from the linear regression analysis to derive the equation Y = a+bX; a and b are parameters; n is sample size; r^2 is square of correlation coefficient; rmse is root mean square error; and P is probability of statistical significance between sex with ns representing $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. TL is total length; SAL is snout to anal-fin insertion length; PL is partial length; TW is total weight; CW is carcass weight.

								P	
Y–X	Species	Sex	n	a (s.e.)	b (s.e.)	r^2	rmse	slope	intercept
TL–SAL	*O. ornatus*	Male	161	44.80 (15.52)	1.16 (0.02)	0.94	19.66	ns	*
		Female	164	71.79 (15.51)	1.12 (0.02)	0.94	21.54		
	O. maculatus	Male	93	26.98 (24.33)	1.22 (0.02)	0.97	25.32	ns	*
		Female	77	41.52 (19.03)	1.20 (0.02)	0.98	16.52		
	O. halei	Combined	236	10.34 (14.17)	1.23 (0.01)	0.98	33.38	ns	ns
TL–PL	*O. ornatus*	Male	113	164.26 (26.42)	1.28 (0.05)	0.86	34.73	ns	***
		Female	124	96.00 (18.76)	1.38 (0.03)	0.93	25.60		
	O. maculatus	Male	63	159.61 (51.08)	1.40 (0.06)	0.90	43.4	ns	*
		Female	60	184.39 (45.98)	1.34 (0.05)	0.91	39.32		
	O. halei	Combined	174	103.97 (23.34)	1.49 (0.02)	0.96	54.63	ns	ns
TW–CW	*O. ornatus*	Combined	73	1.33 (00.14)	1.33 (0.06)	0.87	0.31	ns	ns
	O. maculatus	Combined	93	3.95 (00.75)	1.01 (0.08)	0.61	1.83	ns	ns
	O. halei	Combined	148	1.67 (00.77)	1.53 (0.05)	0.87	3.90	ns	ns

Neonates and small juveniles were rarely caught by commercial wobbegong fishers at any location. Several reasons may account for their absence. Neonates and small juveniles might occupy crevices to avoid predation and forage on small prey living in the crevices. This may provide a physical partitioning of the habitat within a given location. Gear selectivity could also decrease neonate catch because hooks and baits used in the commercial wobbegong fishery are too large. However, gear selectivity is unlikely to explain the absence of larger juveniles because *O. ornatus* of 700–1000 mm TL are commonly caught using the same gear and in the same areas where only a few *O. halei* smaller than 1300 mm TL are caught. It seems more likely that small wobbegongs are not available to the fishery and occur within different

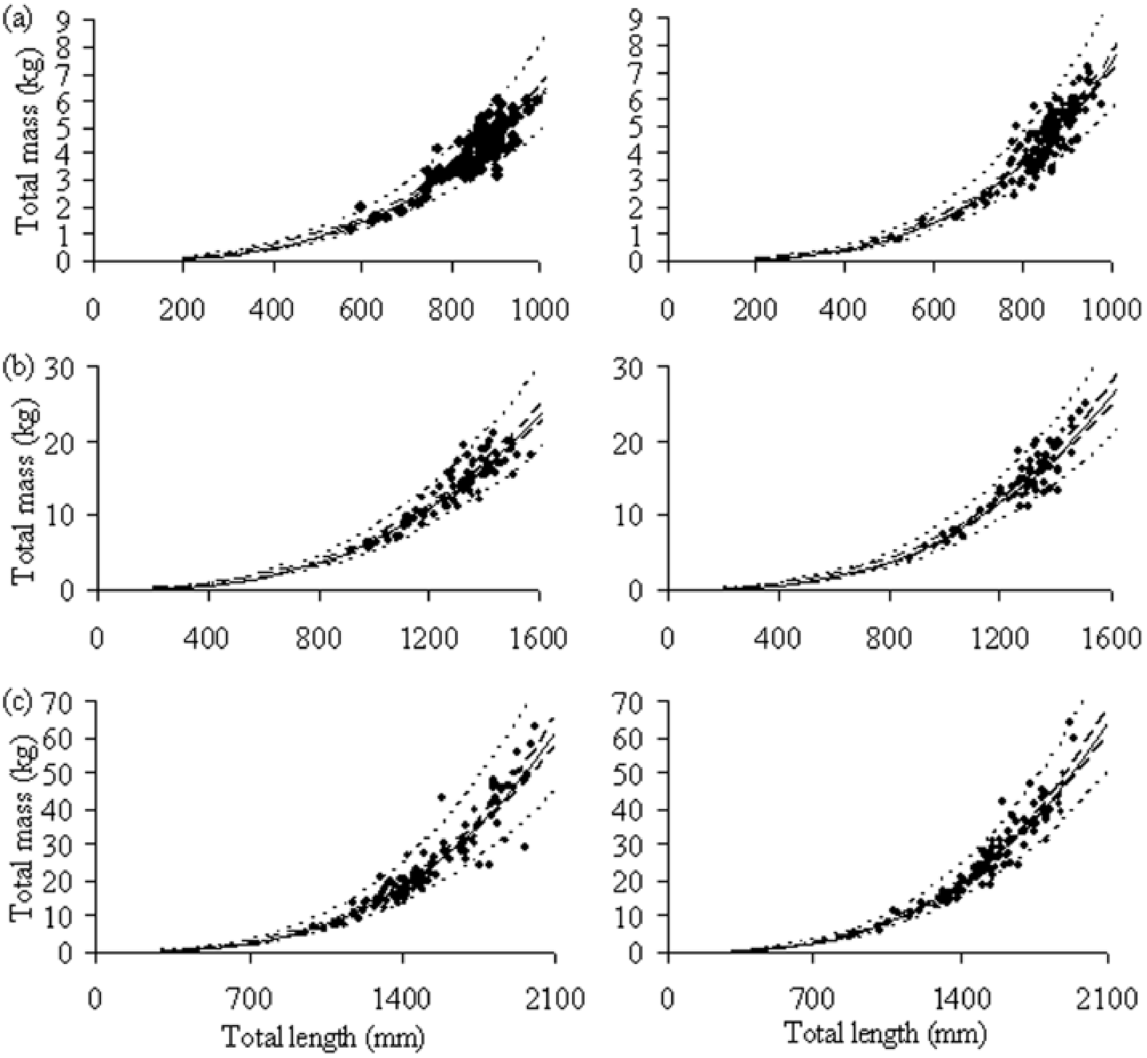

Figure 3. Relationships between total weight and total length of wobbegongs in NSW. Plots of mean total weight against TL (——), with 95% confidence limits (– – –) and 95% prediction intervals (---), for males (left), and females (right) for (a) *O. ornatus*, (b) *O. maculatus*, and (c) *O. halei*. Values for parameters and statistical quantities from regression analysis are given in Table 3.

habitats. Furthermore, a similar study in WA yielded no *O. maculatus* smaller than 900 mm TL and only one *O. halei* (synonym *O. ornatus*) smaller than 1200 mm TL (Chidlow 2003). Size segregation might therefore occur with neonates and small juveniles living in primary and/or secondary nursery areas. Size segregation in habitat use is commonly found in chondrichthyans (e.g. Simpfendorfer 1992), with neonates living in nursery areas for the first weeks, months or years (Heupel and Hueter 2002). Nursery areas are thought to provide neonates and small sharks with increased food availability and/or protection against predators (Heupel and Hueter 2002).

The regression parameters in Tables 2 and 3 are provided for scientists and fisheries managers as an aid to determining size when TL and TW are required but cannot be measured, but where SAL, PL or CW are available. The absence of sex differences in the CW–PL relationships although correlation coefficients are high suggested that somatic growth was similar between males and females (Braccini et al. 2006). However, the regressions of TW on TL differed significantly between males and females with greater body weight in females. Sex-based differences in body weight are often due to discrepancies in the weights of internal organs and are common in

Table 3. Relationships between total weight (TW)–total length (TL) and carcass weight (CW)–partial length (PL). Estimated parameters (and standard error) for the relationships for males and females derived from the equation $TW=acTL^b$ and $CW=acPL^b$; a and b are parameters; c is the Beauchamp and Olson (1973) correction factor; other parameters and statistical quantities as in Table 2.

							P	
Shark category	n	a (s.e. range) x 10^{-9}	b (s.e.)	c	r^2	rmse	slope	intercept
TW–TL								
O. ornatus							*	***
Males	129	21.1 (10.1–44.1)	2.82 (0.11)	1.008	0.84	3.28		
Females	159	1.81 (0.95–3.46)	3.20 (0.10)	1.010	0.88	4.62		
O. maculatus							ns	***
Males	86	57.4 (26.3–125)	2.69 (0.11)	1.008	0.88	2.88		
Females	73	31.7 (12.8–78.3)	2.78 (0.13)	1.007	0.87	2.64		
O. halei							ns	*
Males	86	73.6 (39.2–138)	2.69 (0.11)	1.008	0.88	2.88		
Females	106	6.52 (3.88–11.0)	3.01 (0.070	1.008	0.95	5.21		
CW–PL								
O. ornatus	26	47 (3.12–709)	2.83 (0.43)	1.008	0.9	0.16	ns	ns
O. maculatus	94	1,090 (405–2,920)	2.38 (0.15)	1.019	0.75	0.15	ns	ns
O. halei	149	69.9 (40.8–120)	2.80 (0.08)	1.013	0.64	0.13	ns	ns

chondrichthyans (e.g. Walker 2005). Differences occur due to the inclusion of pregnant females, and the heavier reproductive organs and liver in females (Stevens and Wiley 1986). In contrast, male *O. ornatus* and *O. maculatus* had significantly greater TL for a given SAL and PL compared to females. The reason for this sex difference is unknown.

Most life history parameters used in fisheries assessments are determined as a function of total length or weight. Wobbegongs landed in the NSW Ocean Trap and Line Fishery are, however, beheaded and eviscerated preventing the measurement of total length and total weight. The regression relationships documented in this study allow estimates of total length and total weight to be obtained from landed carcasses enabling future assessments of the ecological sustainability of the fishery through a more accurate knowledge of the catch composition of this fishery. Although many studies provide relationships between total length and total weight (e.g. Stevens and McLoughlin 1991), we concur with recommendations of the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks) (FAO 2000) that future studies should also incorporate the measurement of partial lengths and carcass weight. Only when this is done routinely, will it be possible to estimate, with accuracy, total length and total weight and provide much needed information on the length/weight composition of the catch of shark fisheries.

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Reproductive synchrony of three sympatric species of wobbegong shark (genus *Orectolobus*) in New South Wales, Australia: reproductive parameter estimates necessary for population modelling

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Abstract. Reproductive parameters of three closely-related sympatric species of wobbegong (*Orectolobus ornatus*, *O. maculatus* and *O. halei*) off New South Wales (NSW) were investigated to contribute to a biological basis for the management of a commercial fishery targeting wobbegongs. Estimates of the onset of maturity based on ovary condition were 729 mm, 1117 mm, and 1591 mm total length (TL) for *O. ornatus*, *O. maculatus* and *O. halei* respectively. The length at which 50% of the male population is mature based on clasper calcification was 803 mm, 1282 mm and 1784 mm TL for *O. ornatus*, *O. maculatus* and *O. halei*, respectively, and was similar to female onset of maturity based on uterus condition and to TL-at-maternity. These species of wobbegong had synchronous, triennial reproductive cycles. Follicles took 2 years to enlarge before ovulation. During the first year, follicles remained small, and then grew rapidly during the second year before ovulation during November. Gestation lasted ~10–11 months and parturition occurred during September–October. Mean litter sizes were nine (s.e. 0.5) and 21 (s.e. 1.5) for *O. ornatus* and *O. maculatus*, respectively, and increased with female total length in *O. ornatus*. Pregnant *O. ornatus* and *O. maculatus* were frequently caught in northern NSW and no pregnant wobbegongs, or females with large, yolky follicles were captured south of Sydney. Differences in the reproductive conditions of wobbegongs caught in northern and central NSW suggested geographically dependent reproductive behaviour. Knowledge of the reproductive parameters provided in this paper is necessary for adequate fisheries management and species conservation assessments.

Introduction

Knowledge of the reproductive characteristics of a species is crucial to assess responses to fishing pressure and to estimate sustainable rates of harvest, and is an essential component of most fisheries models. Similarly, reproductive information is essential for evaluating the conservation status of a species with respect to risk of extinction (Hilton-Taylor 2000). Three reproductive components are required for the stock assessment of a fishery: sex ratio at birth, the litter size to maternal length relationship (fecundity), and the relationship between the proportion of the female population in maternal condition (contributing to the next annual recruitment) expressed as a function of shark length (i.e. the maternity ogive) (Walker 2005, 2007).

Wobbegongs (family Orectolobidae) are bottom-dwelling sharks found in tropical to temperate continental waters of the western Pacific (Compagno 2001). Although there are taxonomic uncertainties, eight different species are currently recognised worldwide with three of them inhabiting New South Wales (NSW) waters: *Orectolobus ornatus* (De Vis 1883), *Orectolobus maculatus* (Bonnaterre 1788), and *Orectolobus halei* Whitley 1940 (Last and Stevens 1994; Compagno 2001; Huveneers 2006). Wobbegongs have been commercially targeted in NSW by the Ocean Trap and Line Fishery since 1991 and sold as ‘boneless fillets’ or ‘flake’. The catch has declined from 150 tonnes in 1990/91 to ~70 tonnes in 1999/2000, a decrease of more than 50% in a decade (Pease and Grinberg 1995; NSW Department of Primary Industries, unpubl. data). Concerns that this decline may be indicative of changes in wobbegong abundance along the NSW coast led to wobbegongs (*O. ornatus* and *O. maculatus*) being listed as ‘Vulnerable’ in NSW under the World Conservation Union (IUCN) Red List assessment (Cavanagh *et al*. 2003). This highlighted the need to assess the productivity of wobbegongs and determine their sensitivity to the effects of fishing (Smith *et al*. 1998; Cortés 2002; Mollet and Cailliet 2002).

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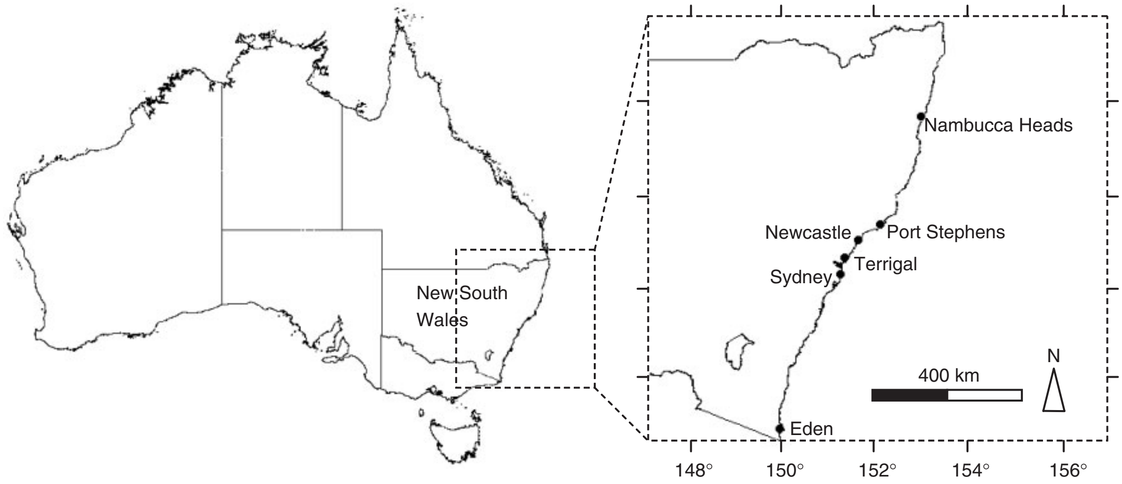

Fig. 1. Sampling locations for collection of wobbegongs in New South Wales.

Despite the commercial importance of wobbegongs in NSW, knowledge of their reproductive characteristics is mostly anecdotal (Last and Stevens 1994; Compagno 2001). A study on four species of wobbegong off Perth, Western Australia (WA) provided reproductive information (Chidlow 2003), but the sample sizes for *O. maculatus*, *O. halei* and *Sutorectus tentaculatus* (Peters 1864) were insufficient to determine their reproductive cycles.

The present study provides information on the reproductive biology and life history characteristics of *O. ornatus*, *O. maculatus* and *O. halei* by investigating various reproductive characteristics including size at birth, total length-at-maturity, total length-at-maternity, gestation period, ovarian cycle, litter size, and sex ratios at or near birth.

Materials and methods

Collection of specimens and biological sampling

Wobbegongs were collected at sea by either hook and line fishing from commercial vessels targeting wobbegongs or by scuba-diving during June 2003–May 2006 at six main locations in NSW (Nambucca Heads, Port Stephens, Newcastle, Terrigal, Sydney and Eden) (Fig. 1). When fishing occurred within three nautical miles, specimens were collected using 10 setlines each with six hooks as regulated by NSW Department of Primary Industries (DPI). When operating further offshore, fishers used up to 110 hooks on one line. Fishers typically used O'Shaugnessy 'J' style hooks size 10/O or 12/O with a wire or nylon trace 50–100 cm long attached to a bottom line by a stainless sharkclip. Lines were set before sunset and hauled at sunrise on the following day. On three occasions, wobbegongs were caught as bycatch in lobster traps set off Nambucca Heads.

Each shark was identified to species (Huveneers 2006) and sex was determined by noting the presence of claspers in males. Before dissection, total length (TL) was measured to the nearest 1 mm, and total mass (TM) and liver mass (LM) were recorded using spring balances. Male and female gonads were excised and held on ice until stored in a freezer at −20°C before further analysis (occurring within 7 days following collection). If females had eggs or embryos *in utero*, they were counted and taken to the laboratory for analysis.

Dissected specimens were visually inspected to assess their reproductive condition and classed using indices adapted from Walker (2005). The reproductive condition of males was based on clasper calcification (CI). The reproductive stage of females was based on two separate indices: a uterus index (UI) reflecting appearance in uterus condition, and an ovary index (OI) based on follicular size and colour (Table 1). Females with extended uterus ($UI = 6$) were pooled with mature females without *in utero* eggs or embryos ($UI = 3$) because of difficulties in distinguishing between *postpartum* and mature uteri in the field, and the biological similarity between these uterus conditions.

In the laboratory, testes were excised from the surrounding epigonal organ, and weighed to the nearest 0.01 g. For females, the single ovary was excised from the surrounding epigonal organ and weighed to the nearest 0.01 g. Follicular colour was recorded as either pale and translucent or yellow and the total number of follicles was counted. Maximum diameter of the three largest follicles and of eggs *in utero* was measured to the nearest 0.1 mm with vernier callipers.

The TL, TM and sex of each embryo in a litter (or sub-sample of a litter), together with the uterus origin (left or right), were recorded for all pregnant sharks. Embryos were defined as 'near-term' if the external yolk sac was not visible.

Male reproduction

The degree of clasper calcification was used to categorise maturity condition (Table 1). Logistic models were used to assess the proportion of males mature at any TL by the method of maximum likelihood of the probit procedure (Walker 2005, 2007). Males were defined as mature if $CI = 3$.

Temporal variation in reproductive condition of mature males was investigated by testing for the effect of month (pooled across years) on the gonadosomatic index ($GSI = 100 \times \text{testes mass} \times (TM)^{-1}$), and the hepatosomatic index ($HSI = 100 \times LM \times (TM)^{-1}$). Testes mass was pooled across locations, because small sample sizes at some of the locations sampled prevented analysis of spatial variation. The effect

Table 1. Indices to stage reproductive condition (adapted from Walker 2005)
CI, clasper calcification; OI, ovary index; UI, uterus index

Organ	Index	Description
Male		
Claspers	CI = 1	Small flaccid claspers with no calcification
	CI = 2	Claspers are flexible, beginning of calcification can be felt
	CI = 3	Claspers are fully calcified
Female		
Ovary	OI = 1	Largest follicle hyaline and not visible without removing epigonal organ
	OI = 2	Largest follicle white, of diameter greater or equal to 5 mm and visible without removing epigonal organ. No evidence of previous ovulation
	OI = 3	Largest follicle yellow and of diameter smaller or equal to 30 mm
	OI = 4	All follicles yellow, of similar size with small epigonal organ and of diameter greater than 30 mm
	OI = 5	Most follicles white and visible without removing epigonal organ. *Corpora lutea* or *Corpora atretica* present in ovary
Uterus	UI = 1	Uniformly thin tubular structure with translucent walls. Indistinct from isthmus
	UI = 2	Thin tubular structure partly enlarged posteriorly. Slight thickening of the walls. Distinction with isthmus start to be visible
	UI = 3	Enlarged tubular structure partly narrow anteriorly
	UI = 4	*In utero* eggs without macroscopically visible embryos
	UI = 5	Embryos macroscopically visible
	UI = 6	Extended uterus

of the month was tested by analysis of covariance (ANCOVA) with TL as a covariate. When the effect of TL was significant, mean GSI was adjusted for the effect of TL by least-squares means.

Female reproduction

Female maturity and maternity ogives were determined the same way as the male maturity ogives using the method of maximum likelihood. Ogives for the onset of maturity were calculated from ovary condition and uterus condition. Females were classed as mature if the follicles were visible without removing the epigonal organ ($OI \geq 2$), or if female uteri were enlarged ($UI \geq 3$). Females were classed as maternal on the basis of UI if, had it survived, it would have contributed to recruitment during the next recruitment season (Walker 2005). For *O. ornatus* and *O. maculatus*, a female was classified in maternal condition if it had eggs *in utero* (UI = 4) during November–December or if it was pregnant with macroscopically visible embryos (UI = 5). Maternity parameters could not be estimated for *O. halei* because of the lack of females sampled in maternal condition. However, multiplying the proportion of maternal specimens by 0.33 provided a similar ogive to the maturity ogive based on the uterus index for each of *O. ornatus* (within 0.01–0.9%) and *O. maculatus* (within 0.2–18.7%). Therefore, the maturity ogive based on the uterus index was adopted to approximate a maternity ogive for *O. halei* by multiplying the proportion of mature specimens based on uterus index by 0.33.

The largest follicle diameter (LFD) measured was used in all statistical analyses because there was no significant difference in the size of the three largest follicles (GLM: $F_{2,911} = 0.54$, $P > 0.05$). The LFD for mature females was plotted against day of year (pooled across years) for each uterus condition separately, following Walker (2005). The largest follicle diameter was pooled across locations because of small sample sizes at some locations; this prevented analysis of spatial variation. In females where UI = 3, two separate reproductive stages were observed at any time of the year: non-pregnant females with small white follicles and non-pregnant females with large yolky follicles. A linear regression of LFD against day of year was undertaken for pregnant females (UI = 5), for females when UI = 3 and follicles were pale and translucent, and for females when UI = 3 and follicles were yolked. The difference in LFD growth between the three reproductive stages of mature females was assessed using ANCOVA, including day of year as covariate.

Paired t-tests were used to test if there was a difference between the number of embryos in the right and left uteri, and if there was a difference between the numbers of male and female embryos pooled across both uteri. The relationship between litter size and maternal length was examined using four different variables: number of embryos, TL of near-term embryos, TM of near-term embryos, and number of ovarian follicles when OI = 4. Each variable was plotted against maternal TL to determine the relationship between litter size and maternal length, and tested using linear regression (Walker 2005). The difference between the number of follicles when OI = 4 and litter size was tested using ANCOVA with TL as covariate.

Results

A total of 904 wobbegongs (435 males and 469 females) was collected and dissected: 385 *O. ornatus* (183 males: 579–995 mm TL; 202 females: 471–1017 mm TL), 185 *O. maculatus* (97 males: 920–1575 mm TL; 88 females: 870–1510 mm TL), and 334 *O. halei* (155 males: 955–2065 mm TL; 179 females: 869–2015 mm TL) (Table 2).

Table 2. Number of wobbegongs caught during June 2003–May 2006

Species	Location	Number caught		
		Male	Female	Total
Orectolobus ornatus	Nambucca Heads	163	170	333
	Port Stephens	20	32	52
	Total	183	202	385
O. maculatus	Nambucca Heads	23	26	49
	Port Stephens	36	21	57
	Newcastle	5	2	7
	Terrigal		2	2
	Sydney	33	37	70
	Total	97	88	185
O. halei	Nambucca Heads	18	13	31
	Port Stephens	5	5	10
	Newcastle	1	2	3
	Terrigal	2	6	8
	Sydney	93	116	209
	Eden	36	37	73
	Total	155	179	334
Total		435	469	904

Male reproduction

Sizes at maturity differed among species (Fig. 2, Table 3). The shortest mature and longest immature shark for *O. ornatus* (790, 860 mm TL) were smaller than for *O. maculatus* (1194, 1360 mm TL), which, in turn, were smaller than for *O. halei* (1684, 1750 mm TL).

The gonadosomatic and hepatosomatic indices of *O. ornatus* differed significantly among months (ANCOVA: $F_{9,99} = 83.25$, $P < 0.001$ and $F_{9,90} = 3.85$, $P < 0.001$ respectively). The gonadosomatic index and HSI showed opposite trends with GSI peaking during March–June, whereas HSI decreased during March–July (Fig. 3*a*).

The GSI of *O. maculatus* differed significantly among months (ANCOVA: $F_{8,41} = 4.13$, $P < 0.01$), whereas the HSI did not differ significantly among months (ANCOVA: $F_{8,23} = 2.17$, $P > 0.05$). Both indices exhibited similar variation through time, being lowest during April–July and increasing to a maximum in January (Fig. 3*b*).

The GSI of *O. halei* differed significantly among months irrespective of whether TL was used as a covariate (ANCOVA: slope $F_8 = 0.25$, $P > 0.05$; intercept $F_1 = 5.44$, $P < 0.05$). The HSI also differed significantly among months (ANCOVA: $F_{6,7} = 4.50$, $P < 0.05$). The GSI of *O. halei* was similar to *O. maculatus* and peaked at about December, then declined to a minimum during March–August. No trend could be detected with the HSI because of large error bars and the absence of data during some months (Fig. 3*c*).

Female reproduction

For all three species, female onset of maturity based on ovary index occurred at a smaller TL than when based on uterus index (Fig. 2, Table 3). Using ovary index as the onset of maturity, lengths of the shortest mature and the longest immature shark for *O. ornatus* (750, 889 mm TL) were smaller than for *O. maculatus* (1035, 1380 mm TL), which, in turn, were smaller than for *O. halei* (1410, 1871 mm TL). The L_{50} for the maternity ogive was larger than L_{50} for the maturity ogive based on ovarian condition for all species (Fig. 2, Table 3).

For *O. ornatus*, follicles were not developing when uterus condition was UI = 1 (i.e. LFD ranged 5–13 mm, mean 8.5 mm, s.e. 0.6 mm, $n = 12$), or when UI = 2 (i.e. LFD ranged 2–17 mm, mean 9.2 mm, s.e. 1.5 mm, $n = 16$). In contrast, the LFD of sharks with UI = 3–5 exhibited more variability. Individuals with UI = 3 had LFD ranging 5–49 mm (mean 17.2 mm, s.e. 1.5 mm, $n = 84$), whereas those with UI = 4 had LFD ranging 5–58 mm (mean 28.7 mm, s.e. 13.4 mm, $n = 4$) and those with UI = 5 had LFD ranging 0–14 (mean 6.7 mm, s.e. 0.4 mm, $n = 35$). Growth in LFD differed significantly among reproductive conditions in mature females (ANCOVA: slope $F_2 = 55.04$, $P < 0.001$; intercept $F_1 = 65.08$, $P < 0.001$; Fig. 4*a*). Mean LFD in pregnant sharks (UI = 5) slowly decreased from ~8 mm to ~3 mm throughout pregnancy (linear regression: $F_{1,34} = 9.38$, $P < 0.01$; Fig. 4*a*, Table 4). The mean LFD of females with pale and translucent follicles (UI = 3), slowly increased from ~7 mm to ~13 mm (linear regression: $F_{1,62} = 14.75$, $P < 0.001$, Table 4). However, large yolky follicles grew much more rapidly than the pale and translucent follicles – their mean LFD increased from ~25 mm to ~57 mm during 12 months (linear regression: $F_{1,62} = 121.44$, $P < 0.0001$; Fig. 4*a*, Table 4). Sharks with eggs *in utero* (UI = 4) were only observed during November. The HSI of *O. ornatus* was correlated with LFD, as well as with embryo TL, indicating an increase of liver mass during follicular development, but a decrease of liver mass during pregnancy (Fig. 5*a*).

For *O. maculatus*, follicles were not developing when UI = 1 (i.e. LFD ranged 5–13 mm, mean 7.0 mm, s.e. 0.4 mm, $n = 13$), or UI = 2 (i.e. LFD ranged 2–17 mm, mean 9.4 mm, s.e. 0.2 mm, $n = 7$). In contrast, the LFD of *O. maculatus* with UI = 3–5 exhibited more variability. Individuals with UI = 3 had LFD ranging 4–51 mm (mean 14.5 mm, s.e. 2.2 mm, $n = 32$), whereas

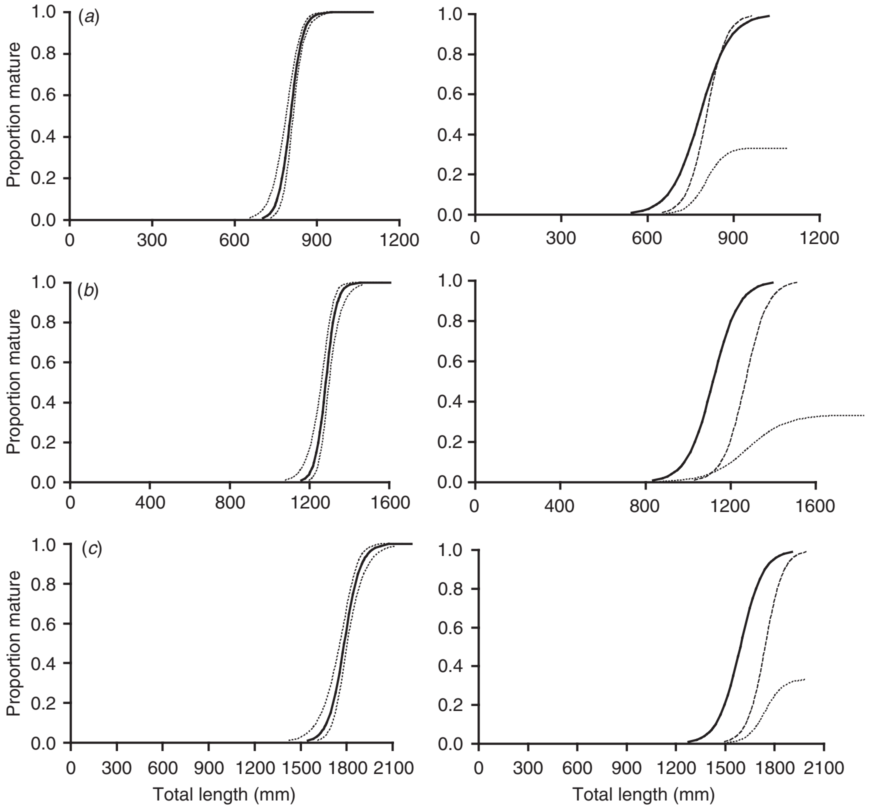

Fig. 2. Total length (TL)-at-maturity for wobbegongs in NSW. (Left) proportion of mature male population based on clasper calcification (——) with 95% confidence limits (----); and (right) proportion of mature female population based on ovary (——), uterus (– – –), and maternal (----) condition for (*a*) *Orectolobus ornatus*, (*b*) *O. maculatus* and (*c*) *O. halei*. Values of parameters and statistical quantities are given in Table 3.

Table 3. Maturity and maternity estimates for wobbegongs in New South Wales

Values for parameters and statistical quantities for the equation $P_L = P_{max}(1 + e^{-\ln(19)(L-L_{50}/L_{95}-L_{50})})^{-1}$; L, total length (TL) measured in millimetres; ML, maximum likelihood; *n*, total number of animals classed as mature; N, total number of animals examined for maturity; *P*, probability of statistical significance; P_L, proportion of animals at TL; L, L_{50} and L_{95}, parameters; P_{max}, asymptotic constant

Sex and species	Ogive	*n*	N	L_{50} (CI)	L_{95} (CI)	P_{max}	ML	*P*
Male								
Orectolobus ornatus	Maturity	143	182	803 (788, 814)	867 (857, 882)	1	−82.71	<0.001
O. maculatus	Maturity	59	96	1282 (1261, 1299)	1360 (1336, 1405)	1	−29.10	<0.001
O. halei	Maturity	51	146	1784 (1758, 1806)	1938 (1902, 2000)	1	−69.79	<0.001
Female								
O. ornatus	Ovarian maturity	173	198	729 (683, 757)	849 (830, 872)	1	−74.54	<0.001
	Uterine maturity	143	198	807 (788, 820)	907 (892, 931)	1	−171.64	<0.001
	Maternity	50	147	805 (796, 811)	901 (893, 911)	0.33	−2454.50	<0.001
O. maculatus	Ovarian maturity	67	79	1117 (1016, 1170)	1297 (1246, 1380)	1	−22.61	<0.001
	Uterine maturity	47	79	1270 (1227, 1296)	1424 (1387, 1504)	1	−56.61	<0.001
	Maternity	14	65	1281 (1255, 1299)	1546 (1496, 1633)	0.33	−317.02	<0.001
O. halei	Ovarian maturity	68	166	1591 (1561, 1616)	1792 (1756, 1843)	1	−96.85	<0.001
	Uterine maturity	64	161	1743 (1724, 1760)	1902 (1869, 1953)	1	−119.15	<0.001
	Maternity	64	161	1743 (1724, 1760)	1902 (1869, 1953)	0.33	−119.15	<0.001

those with UI = 5 had LFD ranging 4–12 mm (mean 6.6 mm, s.e. 0.5 mm, *n* = 13). The mean LFD remained at ~10 mm when UI = 6 and when UI = 3, sharks had pale and translucent follicles (Fig. 4*b*). In contrast when wobbegongs of UI = 3 had large yolky follicles, the mean LFD rapidly increased from ~32 mm to ~55 mm during a 12-month period (linear regression: $F_{1,2} = 92.02$, $P < 0.05$; Fig. 4*b*, Table 4). Finally, the HSI of *O. maculatus* was correlated with LFD, but not with embryo TL (Fig. 5*b*).

For *O. halei*, follicles were not developing when UI = 1 (i.e. LFD ranged 5–13 mm, mean 8.6 mm, s.e. 0.3 mm, *n* = 26), or when UI = 2 (i.e. LFD ranged 2–17 mm, mean 9.4 mm, s.e. 0.3 mm, *n* = 8). In contrast, the LFD of sharks with UI = 3–5 exhibited more variability with LFD ranging 6–52 mm (mean 14.3 mm, s.e. 0.9 mm, *n* = 60). No pregnant (UI = 5) *O. halei* were obtained and one individual with yolky follicles larger than 50 mm LFD was observed. Consequently, growth of the follicles could only be examined in individuals with UI = 3 and pale and translucent follicles. Analysis (linear regression: $F_{1,56} = 11.09$, $P < 0.01$; Fig. 4*c*, Table 4) showed that LFD significantly increased from ~9 mm to ~21 mm. Unlike *O. ornatus* and *O. maculatus*, the HSI of *O. halei* was not correlated with LFD and a possible correlation with embryo TL could not be examined because no pregnant *O. halei* were obtained (Fig. 5*c*).

Forty-three pregnant *O. ornatus* and 13 pregnant *O. maculatus* yielded 236 and 135 embryos, respectively. The embryonic development of *O. ornatus* was similar to that of *O. maculatus*. *In utero* eggs of ~50 mm mean diameter (mass 46 g) were observed during November–December with embryos of ~30 mm TL (0.3 g) visible during January. Embryos reached ~220 mm TL (70 g) in *O. ornatus* and ~230 mm TL (80 g) in *O. maculatus* during September–October when parturition occurred.

For *O. ornatus*, the number of male embryos per uterus (mean 3.1, s.e. 0.4, *n* = 133) did not differ significantly (paired t-test: $t = -1.60$, $P > 0.05$) from the number of female embryos per uterus (mean 3.6, s.e. 0.4, *n* = 156). The number of embryos in the left uterus (mean 4.8, s.e. 0.3, *n* = 208) did not differ significantly (paired t-test: $t = 1.24$, $P > 0.05$) from that in the right uterus (mean 4.6, s.e. 0.2, *n* = 198). For *O. maculatus*, the number of male (mean 8.1, s.e. 1.6, *n* = 106) and female (mean 7.7, s.e. 1.4) embryos per uterus did not differ significantly (paired t-test: $t = 0.6$, $P > 0.05$). *Orectolobus maculatus* also had similar numbers of embryos in the left (mean 10.5, s.e. 0.9, *n* = 137) and right (mean 10.8, s.e. 0.8, *n* = 140) uteri ($t = -0.41$, $P > 0.05$). No pregnant *O. halei* were collected during the sampling period.

Litter size of *O. ornatus* ranged from four to 18 embryos (mean 9.4, s.e. 0.5) and increased significantly in larger females (linear regression: $F_{1,40} = 16.44$, $P < 0.001$; Fig. 6*a*, Table 5). Neither TL nor TM of near-term embryos with sizes 197–222 mm TL (mean 214 mm, s.e. 0.3 mm) from eight pregnant *O. ornatus* were significantly related to maternal TL (linear regressions: TL, $F_{1,6} = 4.92$, $P > 0.05$; Fig. 7*a* and TM, $F_{1,6} = 4.4$, $P > 0.05$; Fig. 7*b*, Table 5). The number of ovarian follicles when OI = 4 ranged from eight to 17 (mean 11.9 mm, s.e. 0.6 mm), and was significantly related to maternal TL (linear regression: $F_{1,15} = 21.98$, $P < 0.001$; Fig. 7*c*, Table 5). However, the number of follicles when OI = 4 was higher than litter size at any TL (ANCOVA: slope $F_1 = 1.02$, $P > 0.05$; intercept $F_1 = 10.24$, $P < 0.01$; Fig. 7*d*). Litter size of *O. maculatus* ranged from eight to 31 embryos (mean 21, s.e. 1.5). However, there was no significant increase in litter size with increasing maternal size (linear regression: $F_{1,11} = 0.55$, $P > 0.05$; Fig. 6*b*, Table 5).

Discussion

Size-at-maturity and -maternity

Total length dimorphism between sexes occurs in many chondrichthyan species, with females exhibiting larger TL-at-maturity and a greater maximum TL-at-maturity than males (Stevens and Wiley 1986; Klimley 1987). The L_{50} for maturity and maximum TL sampled were similar for male and female wobbegongs, suggesting that total length dimorphism between sexes does not occur for these species in NSW. The absence of total length dimorphism between sexes has been previously noted in *O. halei* (synonym *O. ornatus*) and *Orectolobus hutchinsi* (Last *et al.* 2006) in Western Australia (Chidlow 2003).

For *O. halei*, the L_{50} estimated in the present study is similar to a previous estimate of 1750 mm TL (Last and Stevens 1994) and slightly smaller than estimates for *O. halei* in WA (synonym *O. ornatus*: Chidlow 2003). In contrast, estimates for *O. maculatus* from the present study (i.e. 1280 mm TL) differ from previous estimates of maturity of 600 mm TL (Compagno 2001) and ~1000 mm TL in WA (Chidlow 2003). Recent taxonomic evidence suggests the existence of an undescribed species in WA that is similar in appearance to *O. maculatus* in NSW, but matures at a smaller size and has a smaller maximum TL (J. Chidlow and P. Last, pers. comm.). It seems likely that the smaller TL-at-maturity for *O. maculatus* in WA was a result of species misidentification.

The difference of L_{50} obtained from the maturity ogive based on uterus index and the ogive based on ovary index demonstrates the importance of clearly defining maturity when providing a size-at-maturity ogive for a shark species (Conrath 2004; Walker 2005, 2007). For *O. halei*, the calculation of the maternity ogive from the maturity ogive based on uterus condition was undertaken as a result of the lack of females sampled in maternal condition. However, where possible, maternity ogive should be obtained by sampling maternal and non-maternal specimens and then estimated using logistic models (Walker 2005).

Mating period

In NSW, the mating period appears to vary with location. *Orectolobus ornatus* is found primarily in northern NSW and is likely to be mating during April–June, as determined by the increasing GSI during that period. However, two *O. ornatus* were sighted mating on 1 August (S. Hartley, pers. comm.), indicating that the mating period might be slightly longer than indicated by the GSI. The hepatosomatic index has been linked to the reproductive cycle, with liver reserves depleting during the mating period (Rossouw 1987). The hepatosomatic index was lowest during March–July, supporting the mating period suggested by the concurrent peak in GSI. In WA, *O. hutchinsi* and *O. halei* appeared to mate in July (Chidlow 2003), but in NSW *O. maculatus* and *O. halei* seemed to be reproductively active during

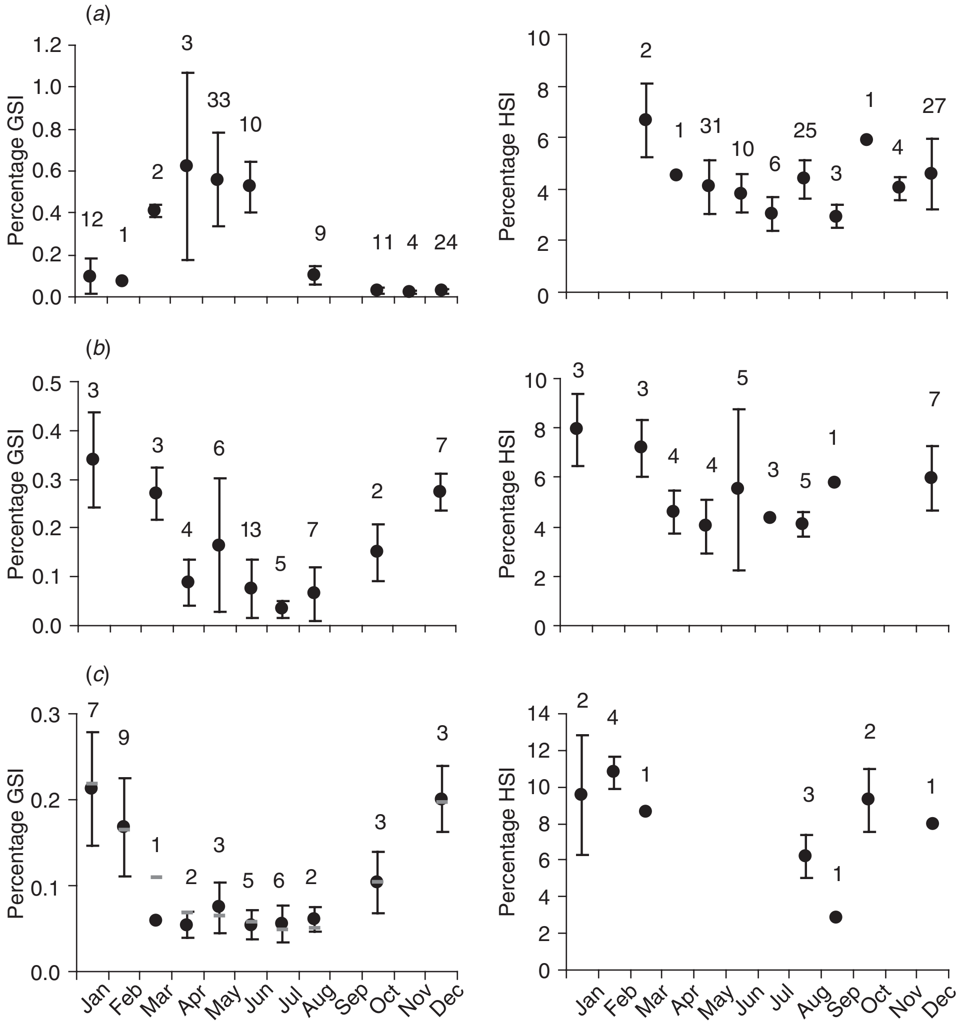

Fig. 3. Temporal variation of male reproductive activity for wobbegongs in New South Wales. Percentage gonadosomatic index (left) percentage hepatic somatic index (right) through month for (*a*) *Orectolobus ornatus*, (*b*) *O. maculatus* and (*c*) *O. halei*. ●, mean monthly value; bars, standard error for monthly value; ▬, mean monthly value corrected for effect of total length of shark; number above bar is monthly sample size.

December–January. However, further studies will be required to elucidate the timing of mating along the NSW coast, and the physiological processes linking masses of testes and liver in wobbegongs.

Ovarian cycle

None of the three species of wobbegong sampled were ovulating. *Orectolobus ornatus* was the only species observed (during November) with eggs *in utero* without macroscopically visible embryos. The existence of individuals within the same population with either large ovarian follicles or completely ovulated eggs during November suggests that ovulation occurs rapidly at this time of year. *Orectolobus maculatus*, *O. halei*, and *O. ornatus* specimens had large ovarian follicles during a similar period, suggesting synchrony between the three species, with ovulation occurring during November in northern NSW.

Follicular growth and the three reproductive stages observed at Nambucca Heads indicated that *O. ornatus* and *O. maculatus* had a triennial ovarian cycle. Within the same population, three reproductive stages of the ovary were observed in mature females: non-pregnant females with ovaries with pale and translucent follicles <20 mm LFD; non-pregnant females with large yolky follicles ≥20 mm LFD; and pregnant females. The two different reproductive stages observed in non-pregnant females indicate that follicles take 2 years to mature following parturition. It also appears that follicular growth occurs at two different rates, which contrasts with previous studies that have assumed constant follicular growth (Walker 2005, 2007; Braccini *et al.* 2006). During the 10–12 month gestation and for the first 12 months after parturition, follicles do not grow. Thereafter, follicles grow rapidly over the following 10–11 months and ovulate at ~50 mm LFD during November. The few *O. halei* collected at Nambucca Heads suggest an ovarian cycle

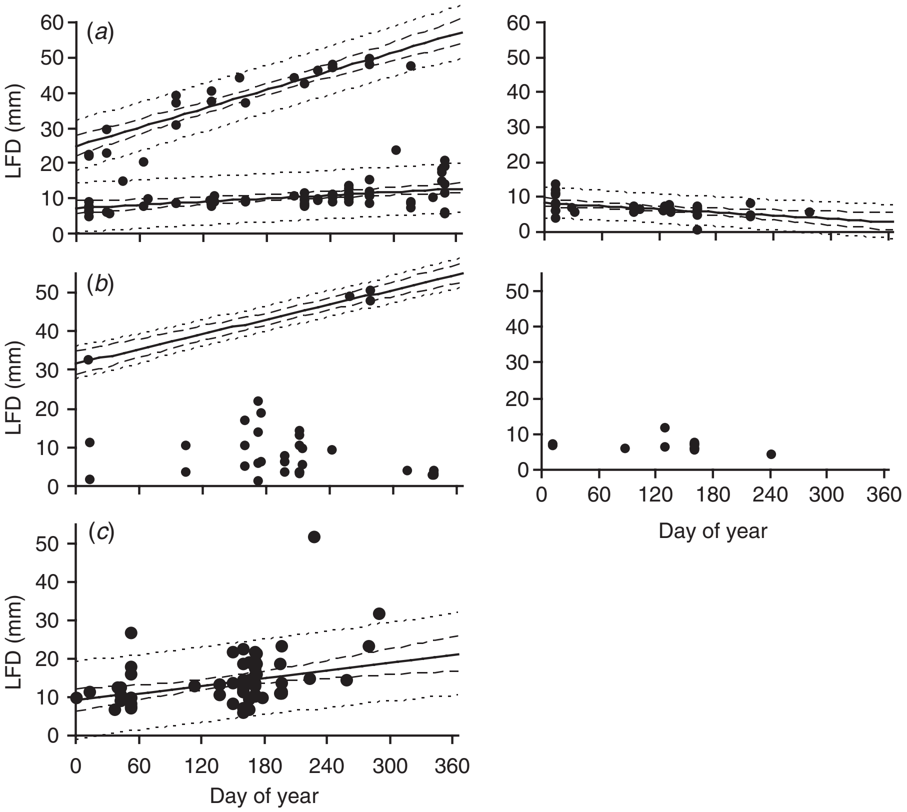

Fig. 4. Largest ovarian follicle diameter against day of year for uterus index (UI) = 3 and 5 of wobbegongs in New South Wales. Largest follicle diameter against day of year for (*a*) *Orectolobus ornatus*, (*b*) *O. maculatus* and (*c*) *O. halei*. Mean largest follicle diameter (——) with 95% confidence limits (– – – –) and 95% prediction limits (-----) are presented. Non-pregnant animals (UI = 3) (left), and pregnant females (UI = 5) (right). Values of parameters and statistical quantities are given in Table 4.

Table 4. Largest follicle growth estimates for wobbegongs in New South Wales

Values for parameters and statistical quantities for the regression equation LFD = a′ + b′t; a′ and b′ are parameters; LFD, largest follicle diameter; *n*, sample size; *P*, probability of statistical significance (*non-significant regression); r^2, square of regression correlation coefficient; rmse, root mean square error for the regression; t, Julian day; UI, uterus index

Species	Uterus condition	N	a′ (s.e.)	b′ (s.e.)	rmse	r^2	*P*
Orectolobus ornatus	UI = 5	35	8.32 (0.64)	−0.015 (0.0049)	2.10	0.22	<0.01
	UI = 3 large	20	24.81 (1.49)	0.089 (0.0081)	3.37	0.87	<0.001
	UI = 3 small	64	7.23 (0.92)	0.023 (0.0035)	2.80	0.19	<0.001
O. maculatus	UI = 5	13	7.52 (1.18)	−0.006 (0.0080)	1.76	0.06	*
	UI = 3 large	4	31.61 (1.57)	0.064 (0.0067)	1.50	0.98	<0.05
	UI = 3 small	28	11.85 (2.06)	−0.010 (0.0098)	4.09	0.04	*
O. halei	UI = 3	58	9.07 (1.55)	0.033 (0.0099)	4.95	0.16	<0.05

synchronous with *O. ornatus* and *O. maculatus*. The period of no follicular growth following parturition may be required for the restoration of energy reserves in the liver enabling subsequent follicular growth as indicated by a rapid increase in HSI with small LFD growth.

Other studies of the reproductive cycles of wobbegongs have been less definitive. In WA, mature female *O. hutchinsi* had the same three reproductive conditions documented as in the present study with 27% of mature females pregnant (Chidlow 2003). Chidlow (2003) suggested a biennial or triennial cycle for *O. hutchinsi*, but could not discriminate between these two alternative hypotheses because of small sample sizes. In NSW, Carraro (2001) proposed a biennial cycle for *O. ornatus* based on behavioural observations of individually identified females over several years. Spatial differences in the duration of ovarian cycles of sharks have been observed and it is plausible that the

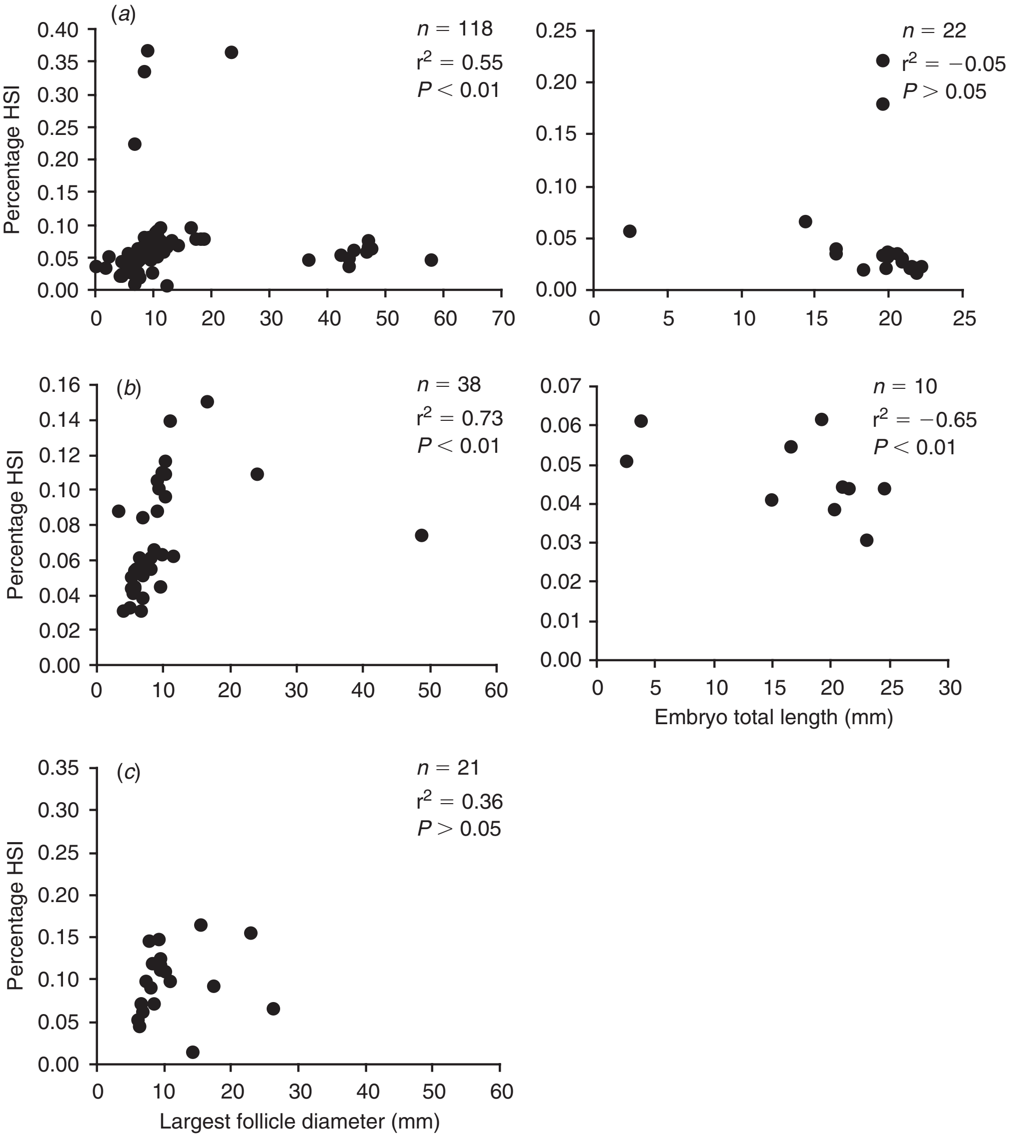

Fig. 5. Percent hepatosomatic index (HIS) against largest ovarian follicle diameter and embryo total length of wobbegongs. Spearman correlation between HIS and ovarian largest follicle diameter (left), and between HSI of pregnant females and embryo total length (right) for (*a*) *Orectolobus ornatus*, (*b*) *O. maculatus* and (*c*) *O. halei*. *n*, sample size; *P*, probability of statistical significance for linear regression; r^2, square of regression correlation coefficient.

ovarian cycles differ between locations. For example, *Mustelus antarcticus* (Walker 2007) and *Mustelus manazo* (Yamaguchi *et al.* 2000) are known to exhibit annual or biennial ovarian cycles depending on particular regions within their entire range. However, dissection of *O. ornatus* collected off Port Stephens during the present study did not support Carraro's hypothesised biennial cycle, because three reproductive stages of mature females were observed at any one time.

Walker (2005, 2007) suggests that the duration of the ovarian cycle is related to the LFD and water temperature. Annual ovarian cycles usually occur in species with a LFD <30 mm, such as *M. schmitti* (Menni 1986) or *Rhizoprionodon terraenovae* (Parsons 1983), whereas biennial species such as *S. acanthias* (Hanchet 1988) and *Notorynchus cepedianus* (Ebert 1986) and triennial species such as *Galeorhinus galeus* (Peres and Vooren 1991; Lucifora *et al.* 2004; Walker 2005), *Squatina guggenheim* (Colonello *et al.* 2007) and *Carcharhinus obscurus* (Branstetter and Burgess 1996; Dudley *et al.* 2005) have LFD ≥40 mm. The long ovarian cycle in chondrichthyans that produce large LFD might be related to the time required for follicles to grow. In wobbegongs, the LFD of all three species was recorded as >50 mm, in line with the generalisation by Walker (2005, 2007). However, other species such as *Triakis megalopterus*, *Carcharhinus limbatus* and *Isurus oxyrinchus* might also have a triennial reproductive cycle, but with a LFD <35 mm (Dudley and Cliff 1993; Smale and Goosen 1999; Mollet *et al.* 2000).

Embryonic development and gestation

Embryos were found until the end of August for *O. maculatus* and the beginning of October for *O. ornatus*, implying that parturition occurred during September–October after a gestation of 10–12 months. The close embryonic development of *O. ornatus* and *O. maculatus* suggests a high concentration of synchrony between these species. Although no pregnant *O. halei* were sampled, a pregnant specimen with near-term embryos was caught off Nambucca Heads by a commercial fisher during September (R. Brislane, pers. comm.), suggesting that *O. ornatus*, *O. maculatus* and *O. halei* have a synchronous period of gestation. In WA, gestation of *O. hutchinsi* was also synchronous with NSW species and lasted 9–11 months (Chidlow 2003). Ovulation, follicular and embryonic development, and parturition occurred simultaneously in *O. ornatus* and *O. maculatus*, and are likely to be similar in *O. halei* (R. Brislane, pers. comm.). Reproductive cycles are thus highly synchronous between these sympatric species.

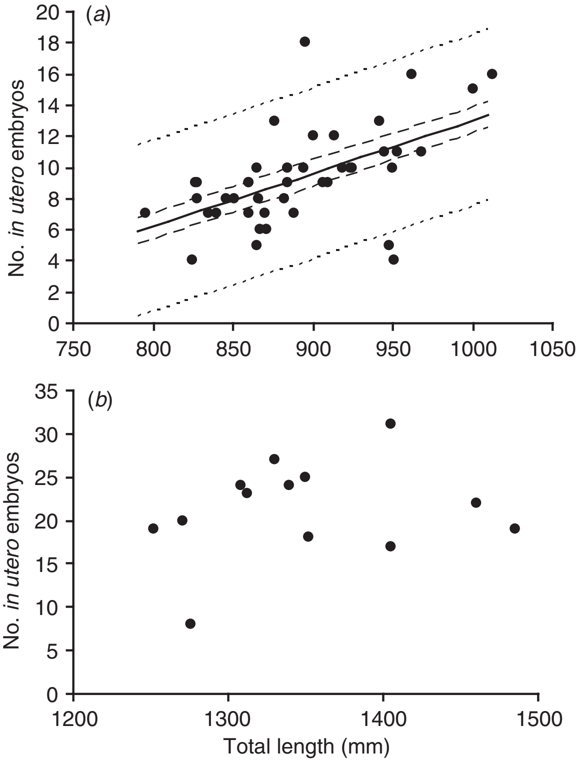

Fig. 6. Relationship between litter size and maternal total length. Mean embryos number (——), 95% confidence limits (– – –), 95% prediction limits (- - - - -), and raw data (•) are plotted against maternal total length of pregnant females uterus index ((UI) = 5) for (*a*) *Orectolobus ornatus* and (*b*) *O. maculatus*. Values of parameters and statistical quantities are given in Table 5.

Litter size–maternal length relationship and fecundity

Orectolobus ornatus had the smallest litter of approximately nine pups and grew to a maximum TL of ~1100 mm. *Orectolobus maculatus* grew to a larger TL and had litters of ~21 pups. Finally, the largest species sampled, *O. halei* had the largest litter at 30–45 pups (R. Brislane, pers. comm.), consistent with the number of enlarged ovarian follicles in a collected specimen and with 36 embryos in a preserved pregnant female specimen in the Queensland Museum (I 16013). In contrast, *O. hutchinsi* has litters of ~23 pups despite having a maximum TL similar to that of *O. ornatus* (Chidlow 2003). Physiological constraints, such as the rate of gas exchange between embryos and uteri (Nammack *et al.* 1985) and other interspecific differences in the structure of the uterine wall (M. Storrie, pers. comm.) may also limit litter size in wobbegongs and explain why *O. hutchinsi* can carry a much larger litter to full term. Litters of *O. ornatus* increased with female TL, but the length of near-term embryo was not related to maternal TL. There was no relationship between litter size and maternal TL in *O. maculatus*. However, the sample size was small and a short pregnant female (1276 mm TL) carried only eight embryos, whereas a large female (1405 mm TL) carried 31 embryos. Further studies may also reveal a significant relationship between litter size and maternal TL in *O. maculatus*.

When litter size and offspring TL are unavailable, the number of large ovarian follicles (OI = 4) can be used as an indication of the number of embryos. Studies comparing fecundity estimated from the number of ovarian follicles with the number of *in utero* embryos have found the former slightly higher than the latter (Marques da Silva and Ross 1993; Lucifora *et al.* 2004; Capapé *et al.* 2005). Fecundity derived from the number of enlarged ovarian follicles in *O. ornatus* is higher than that derived from the number of embryos and is likely a result of the failure of some yolky follicles to ovulate, and subsequent atresia. It is important to note that spontaneous abortions during capture and handling can bias estimates of the number of embryos *in utero*.

Table 5. Fecundity relationships for wobbegongs in New South Wales

Values of parameters and statistical quantities for the equation $P = a' + b'L$; a′ and b′ are parameters; L, maternal total length measured in millimetres; *n*, sample size; No. follicle ovary index (OI) = 4, the number of follicle when females have large yolked follicles >30 mm; *P*, probability of statistical significance for linear regression (*represents non-significant regression); p, fecundity variable; r^2, square of regression correlation coefficient; rmse, root mean square error

Species	p	*n*	a′ (s.e.)	b′ (s.e.)	r^2	rmse	*P*
Orectolobus ornatus	Litter size	42	−20.92 (7.48)	0.034 (0.0084)	0.29	2.69	<0.001
	Embryo TL	8	1.60 (8.93)	0.023 (0.0103)	0.67	1.49	*
	Embryo TM	8	−116.88 (86.83)	0.211 (0.1006)	0.42	6.53	*
	No. follicles OI = 4	17	−29.56 (8.85)	0.046 (0.0099)	0.59	1.75	<0.001
O. maculatus	Litter size	13	−1.77 (31.14)	0.017 (0.0230)	0.48	5.77	*

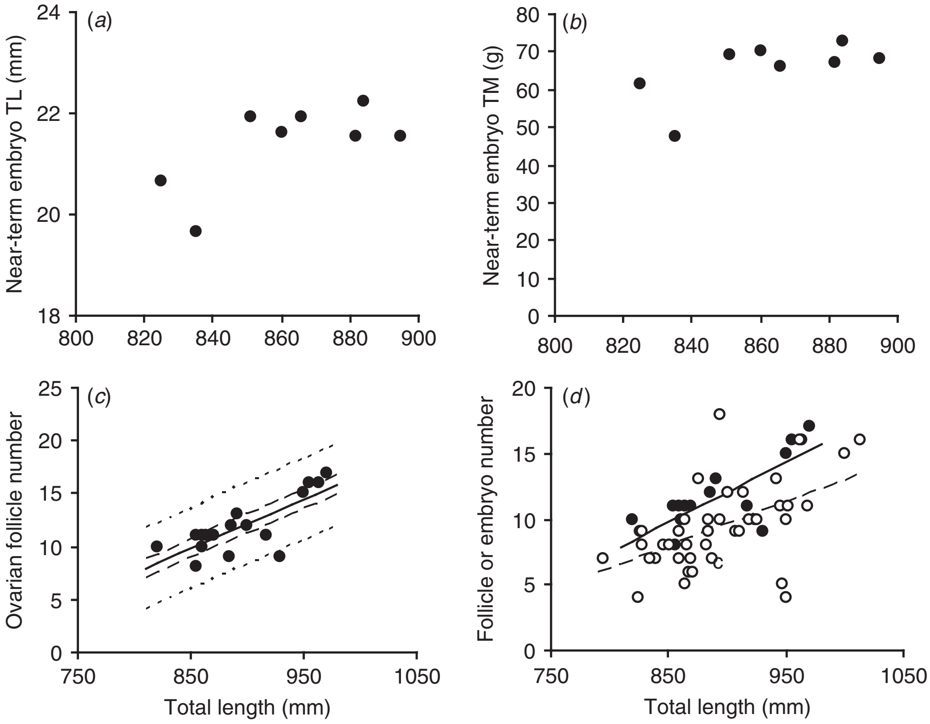

Fig. 7. Relationship between different variables and maternal total length of *Orectolobus ornatus*: (*a*) mean near-term embryo total length (TL); (*b*) mean near-term embryo total mass (TM), and (*c*) mean number of follicle in ovary when ovary index (OI) = 4 (——), 95% confidence limits (– – –), 95% prediction limits (- - - -), and raw data (●) are plotted against maternal total length of females with embryo being classified as near-term when external yolk sac is absent. Values of parameters and statistical quantities are given in Table 5. (*d*) Comparison between the number of ovarian follicles when OI = 4, data (●), regression (——); and the litter size, data (○), regression (– – –) against maternal total length of *O. ornatus*.

Geographical differences

Although pregnant wobbegongs or those with large ovarian yolky follicles were collected in the northern NSW region, females in such reproductive conditions were never caught in the central and southern NSW regions. Furthermore, selected commercial fishers from central and southern NSW, targeting wobbegongs for more than 15 years, have never caught pregnant *O. halei* or *O. maculatus* or individuals with large yolky ovarian follicles (J. Moyce, pers. comm.; S. Fantham, pers. comm.). Although the effects of latitude on life history traits have only been investigated in a few species, increases in growth rate, TL- or age-at-maturity and the size of near-term embryos have been positively correlated with latitude (Yamaguchi *et al.* 2000; Horie and Tanaka 2002; Lombardi-Carlson *et al.* 2003) and reflect the elasticity of these traits. However, geographical variation in reproductive behaviour between locations only 500 km apart has not previously been observed in chondrichthyan species. Several alternate explanatory models may account for the absence of reproductively active female wobbegongs off Sydney and sites to the south. First, wobbegongs may stop feeding during mating periods as observed in captive *O. ornatus* (N. Otway and M. Storrie, pers. comm.), limiting their capture by baited setlines. Second, as hypothesised for *G. galeus* (Walker 2005), female wobbegongs may migrate to warmer, northern waters to increase rates of follicular and embryonic development. Third, female wobbegongs may move to locations where targeted fishing does not occur (e.g. estuaries or offshore locations). Locating pregnant and *postpartum* females and investigating their movements through acoustic tagging may elucidate the whereabouts of reproductively active females around and south of Sydney and complete our understanding of wobbegong reproductive behaviour.

Scientists are able to use reproductive parameter estimates in fishery models to create necessary species-based risk assessments and inform future management decision. The present investigation provides fishery managers with the required information and parameters (e.g. sex ratio and fecundity) needed to create stock assessment models and determine resilience to the current fishing level pressure.

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Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroselachus crepidater*

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Abstract: Bands on the external surface of the second dorsal-fin spine proved to be a novel method of estimating the age and growth of *Centroselachus crepidater*. Bands that followed the shape of the spine base were enhanced with an alizarin red derivative. Internal bands in spine cross sections were also examined. The number of both external and internal bands increased with animal size, although most spines had more external than internal bands. External bands were more reliable and were assumed to be annuli. The rate of band formation differed after five bands had been formed, and internal bands ceased forming after 30 years. Females to 54 years old and males to 34 years old were examined. Maturity occurred over a wide age range, with estimates of 20 years for females and 9 years for males. The youngest pregnant female was 27 years old. The Francis reparameterized von Bertalanffy growth model found similar growth for males and females, and the von Bertalanffy equations were $L_t = 96.12(1 - e^{(-0.072(t+6.13))})$ for females and $L_t = 73.22(1 - e^{(-0.141(t+2.99))})$ for males.

Résumé : L'étude des bandes sur la surface externe de la seconde épine dorsale s'est avérée être une nouvelle méthode d'estimation de l'âge et de la croissance chez *Centroselachus crepidater*. Nous avons accentué le contraste des bandes qui suivent la forme de la base de l'épine à l'aide d'un dérivé du rouge d'alizarine. Nous avons aussi examiné les bandes internes sur des coupes transversales d'épines. Le nombre de bandes, tant externes qu'internes, augmente en fonction de la taille de l'animal, bien que la plupart des épines portent plus de bandes externes qu'internes. Les bandes externes sont plus fiables et nous considérons qu'il s'agit d'annulus. Le taux de formation des bandes est différent après la formation des cinq premières bandes et la formation de bandes internes cesse au bout de 30 ans. Nous avons examiné des femelles d'âge maximal de 57 ans et des mâles de 34 ans. La maturité est atteinte sur une gamme étendue d'âges et nous estimons l'âge de la maturité à 20 ans chez les femelles et de 9 ans chez les mâles. La femelle gravide la plus jeune avait 27 ans. Le modèle de croissance de von Bertalanffy avec les paramètres déterminés par la méthode de Francis indique une croissance semblable chez les mêles et les femelles; les équations de von Bertalanffy sont L_t des femelles = $96,12(1 - e^{(-0,072(t+6,13))})$ et L_t des mâles = $73,22(1 - e^{(-0,141(t+2,99))})$.

[Traduit par la Rédaction]

Introduction

Deepwater dogfishes are a major bycatch component of many of the world's demersal fisheries, and several species are directly targeted for the shark fillet and liver oil markets. In Australia, deepwater dogfishes are primarily caught as byproduct to demersal trawl fisheries, and the estimated annual value of deepwater dogfishes exceeds AU$1.5 million (Daley et al. 2002). In 2005, eight species of deepwater dogfishes, including the golden dogfish, *Centroselachus crepidater* (Bocage and Capello 1864), became managed under a "basket" quota system, with a total allowable catch set at 200 tonnes (P. Shoulder, Australian Fisheries Management Authority, P.O. Box 7051, Canberra Business Centre, ACT, Australia 2610, personal communication).

Centroselachus crepidater is uniformly dark brown to black, with a slender body, long snout, and small dorsal-fin spines. It occurs on the continental and insular slopes in depths of 270–1300 m in the eastern Atlantic (Iceland to southern Africa), the Indian Ocean (Aldabra Islands and India), the eastern Pacific (northern Chile), and western Pacific and eastern Indian oceans (New Zealand and southern Australia) (Last and Stevens 1994).

Age information forms the basis for the calculations of growth rate, mortality rate, and productivity, making it one of the most influential biological variables for estimating

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population status and assessing the risk associated with exploitation (Ricker 1975; Musick et al. 2000; Campana 2001). Band counts from vertebrae are the most commonly used method for ageing elasmobranchs (Cailliet and Goldman 2004), although most dogfish vertebrae are poorly calcified with no visible banding (Jones and Geen 1977).

Kaganovskaia (1933) first used the second dorsal-fin spine to age the spiny dogfish (*Squalus acanthias*), and the structure and function of dorsal-fin spines has since been documented (Maisey 1979; McFarlane and Beamish 1987). *Squalus* species often have spines with a banding pattern on an enamel cap, and these bands are more commonly used to age dogfishes (Holden and Meadows 1962; Nammack et al. 1985; McFarlane and Beamish 1987). However, most deepwater dogfish spines do not possess an enamel cap, and Tanaka (1990) reported an alternative ageing technique using an internal banding pattern in the spine cross sections (hereafter called "internal bands"). Over the past decade, these internal bands have been used to age several deepwater dogfishes (e.g., Tanaka 1990; Guallart Furio 1998; Clarke et al. 2002*b*). However, most studies report the usefulness of spines as a tool for ageing rather than estimating growth, and the validation of deepwater dogfish age estimates has never been attempted.

Holden and Meadows (1962) were the first to note the growth bands on the stem of the *S. acanthias* spine. In this species, each band followed the shape of the spine base and could only be counted after removing the enamel cap. The number of these external bands matched the number of enamel bands. However, because of the relative ease in counting bands on the enamel cap, the use of external base bands (hereafter called "external bands") has not been investigated.

Holden and Meadows (1962) suggested that spine growth resembled the stacking of paper cups. However, the growth of the *C. crepidater* spine is assumed to be similar to that of *S. acanthias* as described by Beamish and McFarlane (1985). In this case, upward growth is caused by deposition of dentine at the spine base, and outward spine growth is caused by the production of cartilage and dentine at the spine centre. Therefore the formation of external bands (and enamel bands) is independent of inner dentine band formation.

This study reports an alternative method of ageing deepwater dogfishes and constitutes the first investigation into the age and growth of any deepwater shark in the southern hemisphere. More traditional ageing methods using internal bands were also tried, and the results were compared with those of our technique.

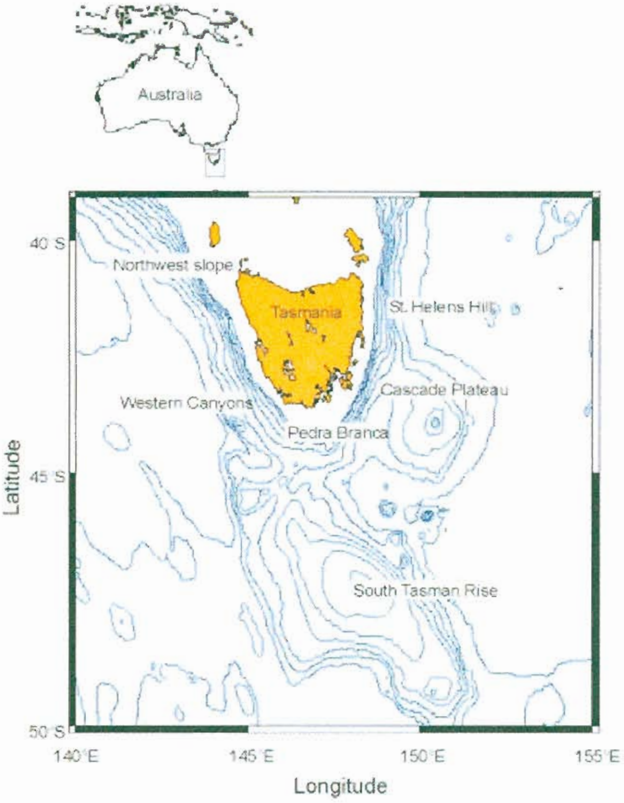
Materials and methods

Sample collection

Between November 2000 and July 2002, *C. crepidater* were opportunistically collected from the bycatch of commercial fisheries operating in southeastern Australia (Fig. 1). Fishers were primarily targeting orange roughy (*Hoplostethus atlanticus*) and most *C. crepidater* were collected from depths of 650–1000 m.

Each dogfish was sexed, and the total length (TL) and fork length (FL) were measured (±1 cm) by allowing the caudal fin to take a natural position. All animal lengths hereafter are TL. For those dogfishes with a damaged caudal fin, FL was converted to TL using TL = 1.08FL + 2.74 ($n = 360$, $r^2 = 0.99$). Dogfishes were weighed (±10 g) on a top-loading digital scale, and the relationship between weight and length was examined. Embryos were weighed to the nearest 0.1 g and length was measured to the nearest 0.1 cm.

Fig. 1. Topographic map of southeastern Australia indicating the six fishing locations where *Centroselachus crepidater* specimens were collected.

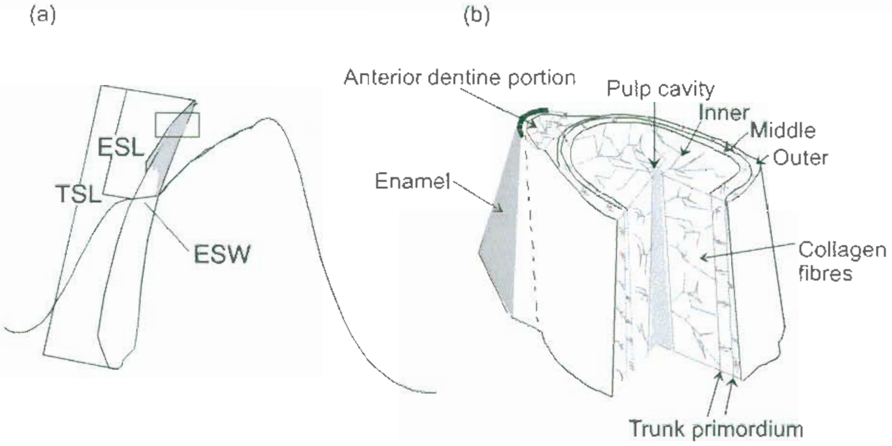


Spine preparation

Preliminary investigations found that the first dorsal-fin spines were more often damaged compared with the second dorsal-fin spines; therefore, second dorsal-fin spines were chosen for further examination. Second dorsal-fin spines were collected by cutting towards the vertebral column. Care was taken to include the delicate base portion. Spines were labelled and stored frozen for later examination.

Most of the muscle and connective tissue was removed from each spine using a sharp scalpel. Spine morphometrics (Fig. 2*a*) were measured using digital calipers (±0.01 mm). The external spine length (ESL) was measured from the tip of the spine to the point of entry into the flesh, and external spine width (ESW) was the diameter of the spine at this point of entry. Spines were thoroughly cleaned by repeatedly douching in hot tap water for a few seconds and then lightly scrapping with a blunt dental tool. Total spine length (TSL) was measured from the spine tip to the anterior side of the spine base. These morphometrics were used to examine spine

Fig. 2. (*a*) Dorsal fin spine illustrating morphometric measurements: total spine length (TSL), external spine length (ESL), and external spine width (ESW). (*b*) Internal structure of a dorsal-fin spine illustrating the three (inner, middle, and outer) dentine layers.



growth by investigating their relationship with animal size. Spines were kept wet or frozen until all external age analysis had been completed.

External base bands were enhanced by soaking in a solution of saturated alizarin red in 1% potassium hydroxide (KOH) at a ratio of 1:100 (1% *v/v*) for 3–5 days. After the first 24 h, the internal cartilage rod could be removed easily. Spines were rinsed in tap water and were either examined immediately or stored frozen. Band clarity could be increased by lightly polishing with wet fine-grade abrasive paper. All spines were examined under a low-power (6×) dissecting microscope, with a magnifying lamp, by the naked eye, or a combination of all three depending on the particular spine.

One external band describes either a ridge of enamel or a white band after rubbing a stained spine with wet abrasive paper. Counting started at the spine base and some spines showed better band clarity along the posterior edge. Staining did not always enhance bands on spines from younger or faster-growing fish, as the bands were widely spaced and ridges were less obvious. In some older fish, bands near the base were very tightly packed and could only be identified on the posterior margin of the spine.

On completion of all external band examination, the base of the spine was "plugged" with plasticine and placed laterally in Wonderflex® silicon cookware "brownie" molds and embedded in epoxy resin (Renlam M-1 AU resin and HY951 hardener at 9:1 *w/w*). Plugging the spine base prevented resin from moving into the pulp cavity, which could cause damage to the internal spine structure. About 5–15 transverse sections were taken from the tip of each spine using a lapidary saw (rpm = 1250) fitted with a diamond-tipped 0.6 mm wide blade. Section thickness was measured (±50 μm) with digital callipers and was generally 250–350 μm. The internal spine structure consists of three dentine layers: outer, middle, and inner (Fig. 2*b*). However, the internal dentine layer was much wider than the two other layers and had the clearest bands. The optimal sectioning point was immediately below the apex of the pulp cavity. Spine sections were mounted onto glass slides using epoxy resin. Slides were placed in a 35 °C oven until the resin had set (usually taking 1–2 h).

Bands are formed simultaneously in each of the three dentine layers (McFarlane and Beamish 1987). Band spacing is widest in the inner layer, and therefore, only bands in the inner dentine layer were counted. Counting started at the pulp cavity (spine centre) and continued outwards until the first trunk primordium (the junction between the inner and middle layers). One internal growth band refers to a dark (opaque) and light (translucent) concentric band.

Reading precision and accuracy

Three nonconsecutive band counts were made for each spine without prior knowledge of the animal's length or sex or the previous band counts. A subjective measure of band readability was used: the sliding scale started at 1 (samples with unambiguous bands with excellent readability) to 5 (unreadable sample). An independent reader was not available, and therefore, approximately 20% of the samples were reexamined 1–3 months after the first examination to imitate the second (independent) reader protocol suggested by Cailliet and Goldman (2004).

Precision was calculated using the coefficient of variance (CV) across all fish ages following Campana (2001). Calculating CV gave an assessment of the ease of ageing dogfish spines and tested the within-reader reproducibility of age determinations. Samples were discarded if the readability score was >3, and an upper limit for CV was set at 20% for each spine section (adapted from the index of average percent error (IAPE) for vertebrae analysis; Beamish and Fournier 1981). Samples were not included in the analysis if the CV was >20%. The average of the mean age for each of the three counts defined the age estimate for each shark (Casey et al. 1985).

Verification

The annual periodicity of internal bands was investigated by edge analysis and marginal increment analysis. An edge-grading system adapted from Yudin and Cailliet (1990) was applied for edge analysis. The condition of the growing edge of the inner dentine was examined under 60× to 100× magnification and was related to the season of capture. Edges were recorded as translucent, narrow opaque, or wide opaque. The observed and expected ratios of translucent to opaque last bands for each season were then compared using chi-square (χ^2) tests.

The marginal increment ratio (MIR) was calculated from transverse spine sections with 16–19 internal bands, where the width of the ultimate band (w_b) was expressed as a proportion of the penultimate band (w_{b-1}). All measurements (μm) were made using the F-View Soft Imaging System (SIS, 8 Timbertop Crt., Gulfview Heights, SA 5109, Australia; www.soft-imaging.net) on a BX51 Olympus compound microscope with a differential interference contrast. The radius of the inner dentine section was used to ensure that sections from the same regions were examined. Measuring the marginal increment in the inner dentine was difficult. Extremely thin (<300 μm) sections were required to ensure that the depth of field was minimised at high magnification. Mean MIR ± 1 standard error (SE) was plotted seasonally to locate periodic trends in band formation. If the translucent zones are formed annually, the MIR should decline once each year (i.e., when the new opaque zone starts to form outside the translucent zone). Analysis of variance (ANOVA) was performed to detect any significant differences in the MIR throughout the year.

The length-at-age data and growth curves were compared with published ages from radiometric isotope analysis of vertebrae for five female *C. crepidater* from southern Australia (Fenton 2001).

Growth

The von Bertalanffy growth model (VBGM) is commonly use to represent fish growth, although it does not always provide a particularly good fit and there has been a wide array of criticisms (Haddon 2001). Moulton et al. (1992) adopted the Francis (1988) reparameterized VBGM equation (eq. 1) for shark age and growth analysis to correct for the effects of gillnet length-selective sampling bias. The reparameterized equation was subsequently used to test for the biasing effects of gillnet length-selective fishing mortality (Walker et al. 1998):

$$(1) \qquad L = l_\phi + (l_\psi - l_\phi)(1 - r^{2(T-\phi)/(\psi-\phi)})/(1 - r^2)$$

where the three von Bertalanffy (1938) parameters (L_∞, t_0, and k) are replaced with l_ϕ (mean length at reference age ϕ), l_ψ (mean length at reference age ψ), l_χ (mean length at reference age $(\phi + \psi)/2$)), and $r = (l_\psi - l_\chi)/(l_\chi - l_\phi)$. The same reference ages (ϕ and ψ) were chosen for males and females within the range of the data to avoid unnecessary extrapolations and to allow direct comparisons between male and female growth.

The Francis model was used to examine growth for each sex, and the Francis parameters were related to the conventional von Bertalanffy parameters using

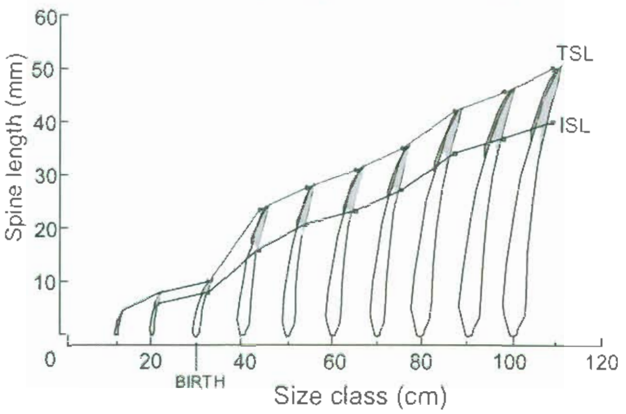
$$(2) \qquad L_\infty = l_\phi + (l_\psi - l_\phi)/(1 - r^2)$$

$$(3) \qquad k = -(2 \log_e r)/(\psi - \phi)$$

$$(4) \qquad t_0 = \phi + (1/k) \log_e((L_\infty - l_\phi)/L_\infty)$$

Confidence intervals (95%) around the Francis parameters gave a direct measure of the heterogeneity in length at age. Confidence intervals for both Francis and VBGM parameters were calculated using the nonlinear regression function in Systat 8.0® (Systat Software Inc. 1999).

Fig. 3. Relationship between animal size and mean second dorsal-fin spine length (total spine length, TSL; internal spine length, ISL) for male *Centroselachus crepidater* from southeastern Australia. (Shaded portions indicate spine pigmentation; see Fig. 4.)



Francis growth parameters were directly compared, although χ^2 tests on each likelihood ratio were used to compare the data between sex and external versus internal band counts. This method, advocated by Kimura (1980), Moulton et al. (1992), and Haddon (2001), is a more reliable means of finding a difference in growth. Chi-squared tests were performed in Microsoft Excel® as outlined by Haddon (2001).

The relationship between external and internal band counts was investigated by regression analysis using the nonlinear (mode/loss) regression function in Systat 8.0® (Systat Software Inc. 1999).

Longevity

Longevity was assumed to be the maximum number of external band counts.

Age at maturity

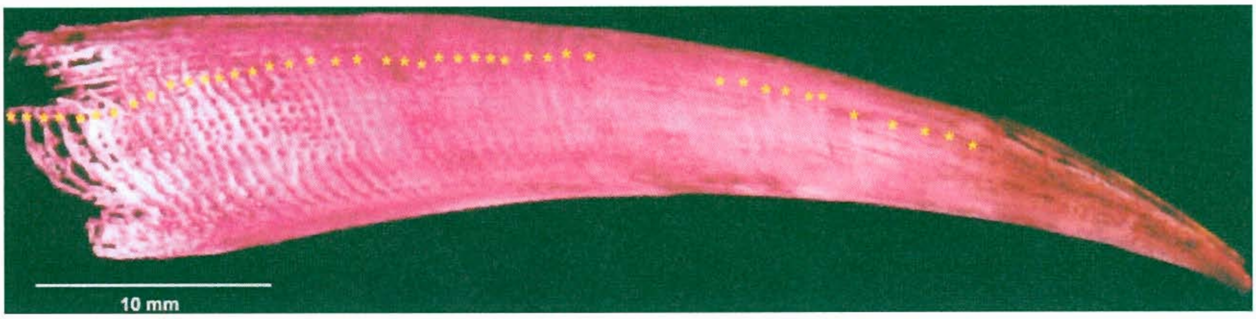
Sexual maturity in males was determined by clasper condition (elongation and calcification) and macro-examination of the testes. Males were considered mature once claspers had fully calcified and testes showed signs of lobulation. The reproductive status of females was based on the condition of the ovaries and uteri adapted from Wetherbee (1996) and Stehmann (2002). Females were assumed in a mature condition when distinct oocytes were present in the ovaries and (or) the uteri had expanded away from the central axis of the body cavity.

The age at maturity (A_{50}) was estimated from the relationship between the proportions of mature versus immature specimens within 5-year age classes. Each interval was indicated by its lower value. A logistic curve was fitted for each sex using probit analyses.

Results

The relationship between weight (W) and total length (TL) differed significantly with sex ($p < 0.05$): male, $W = 0.001\ \mathrm{TL}^{3.434}$ ($r^2 = 0.67$, $n = 154$); female, $W = 0.002\ \mathrm{TL}^{3.234}$ ($r^2 = 0.86$, $n = 238$). Length ranges were 30–79 cm for

Fig. 4. Second dorsal-fin spine of *Centroselachus crepidater* stained with alizarin red and potassium hydroxide to enhance the external banding pattern (each asterisk (*) represents one band; scale bar = 10 mm).



males and 29–99.5 cm for females. The length frequencies indicate sexual dimorphism, with females attaining a larger size.

Spine structure and growth

The first and second dorsal-fin spines of *C. crepidater* are similar in size and structure. Each spine is slightly curved and the portion beneath the skin is ivory in colour, whereas the external portion is usually dark brown. A small strip of enamel covers the anterior dentine portion, and no other enamel is present on the spine surface. The cartilage rod that supports the spine is about two-thirds of the total spine length.

Spines were visible in embryos >10 cm TL, and full-term embryos (~30 cm TL) had fully developed spines measuring 8–9 mm TSL. A total of 344 second dorsal-fin spines were collected and measured, of which 267 had no damage, 55 had a worn or blunt tip, 18 had a broken tip, and four were broken and therefore discarded. The relationship between TL and TSL for nondamaged spines was linear and differed significantly between sexes ($p < 0.05$, $F = 9.98$): male, TL = 1.60 TSL + 16.02 ($r^2 = 0.67$, $n = 113$); female, TL = 1.12 TSL + 29.44 ($r^2 = 0.59$, $n = 142$).

Approximately 75% of the spine was beneath the skin. Spine growth was most rapid between 30 cm (birth) and 40 cm TL (Fig. 3), and the linear correlation strengthened significantly ($r^2 = 0.99$) after 40 cm TL for both sexes.

External bands

The external surfaces of 257 second dorsal-fin spines were examined for growth bands. A countable banding pattern (Fig. 4) was found on the surface of 241 (94%) spines. Overstaining was the main cause of poor readability, and most spines had a readability score of 1 or 2. The average reading precision (CV) of readable counts was 4.04%. Ten ages had a CV above 20% and were excluded from all age analyses. The number of bands did not influence readability, and there was very poor correlation ($r^2 = 0.054$, $n = 229$) between the number of bands and the coefficient of variance.

The number of external bands increased with animal size, and no bands were found close to the spine tip. The greatest number of bands observed was 54 (99 cm TL) for females and 34 (70 cm TL) for males. The largest female (99.5 cm TL) had 37 bands, and the largest male (79 cm TL) had 26 bands. Near-term embryos had no external bands, and a birth-band subtraction to estimate age was not required. The

Fig. 5. Reparameterized von Bertalanffy growth (VBG) curves generated from (*a*) external spine data for male (M, solid circles, $n = 86$) and female (F, open circles, $n = 146$) and (*b*) internal spine data for male (M, solid circles, $n = 69$) and female (F, open circles, $n = 100$) *Centroselachus crepidater* from southeastern Australia. Individual VBG and Francis parameters are given in Table 1.

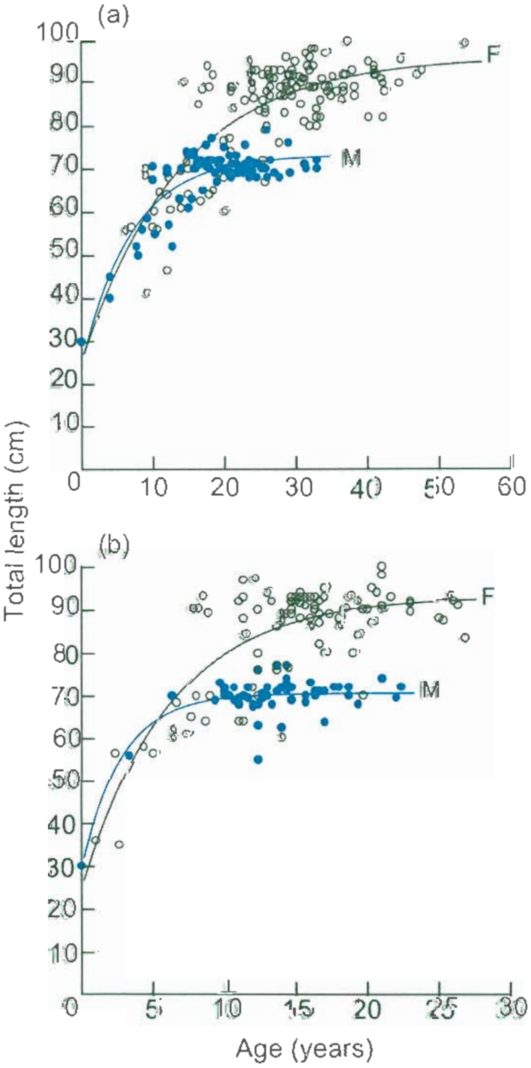


Table 1. Estimates of the von Bertalanffy (1938) and Francis (1988) growth parameters (including upper and lower 95% confidence limits) for male and female *Centroselachus crepidater* from southern Australia.

		External bands		Internal bands	
Parameter		Male (n = 86)	Female (n = 146)	Male (n = 69)	Female (n = 100)
von Bertalanffy					
L_∞ (cm)	Estimate	73.2	96.1	70.6	93.2
	Upper	75.2	100.9	71.8	97.4
	Lower	71.2	91.6	69.3	88.9
k (year^{-1})	Estimate	0.141	0.072	0.362	0.163
	Upper	0.173	0.092	0.509	0.211
	Lower	0.109	0.052	0.215	0.116
t_0 (year)	Estimate	−2.99	−6.13	−1.51	−1.92
	Upper	−1.49	−4.59	−0.66	−0.49
	Lower	−4.47	−8.17	−2.36	−3.34
Francis					
l_2 (cm)	Estimate	37.6	42.6	50.8	45.9
	Upper	41.9	54.1	56.2	52.7
	Lower	33.2	31.1	45.3	39.1
l_{12} (cm)	Estimate	69.1	82.3	70.1	85.4
	Upper	69.9	85.4	71.0	97.3
	Lower	68.3	79.2	69.1	88.9
l_{22} (cm)	Estimate	73.2	96.3	70.6	93.2
	Upper	75.2	100.9	71.8	97.4
	Lower	71.2	91.6	69.3	88.9
r^2		0.75	0.78	0.73	0.66

Note: L_∞, asymptotic length; k, growth coefficient; t_0, age at length 0; r^2, coefficient of determination; l_2, mean total length (TL) at age 2; l_{12}, mean TL at age 12; l_{22}, mean TL at age 22.

base of larger (older) spines was fragile and was often only partly formed.

Assuming external bands are formed annually, the reparameterized VBGM was fitted to length-at-age data for each sex (Fig. 5*a*; parameters are listed in Table 1). The Francis parameters show that males grow about 32 cm from the ages of 2 to 12, whereas females grow 40 cm over the same period. However, males only grew a further 4 cm over the next 10 years (between 12 and 22 years) compared with 14 cm for females.

Kimura's likelihood ratio test calculated a difference in the growth curves for male and female *C. crepidater*. A strong difference between the L_∞ of each sex was indicated (p = 0.009), whereas there was no indication that the t_0 and k parameters differed significantly (p = 0.569 and 0.122, respectively).

The number of external bands ranged from 0 to 54 years for females and from 0 to 33 years for males. However, most females were 24–34 years, whereas males 16–24 years were more common.

Internal bands

Cross sections of 201 spines were examined, and the inner dentine layer contained the most distinguishable banding pattern (Fig. 6). The optimal sectioning location (where band clarity was the best) was where the inner dentine was the widest; this corresponded to a region ~5 mm from the tip in unworn adult spines. Sections close to the tip had poor band clarity and the middle to outer layers were very narrow.

The number of internal bands increased with animal size, and the greatest number of bands observed was 27 (83 cm TL) for females and 22 (72 cm TL) for males. The spines of the largest female (99.5 cm TL) and male (79 cm TL) examined had unreadable internal bands. The largest female with readable internal bands (93 cm TL) had 21 bands, whereas the largest male with readable bands (77 cm TL) had 14 bands.

The mean CV of these bands was 7.7%, and 32 spines (15%) were excluded because of poor readability or poor

Fig. 6. Inner dentine layer from the spine of an 83 cm female *Centroselachus crepidater* with 25 bands. Measurements (µm) for marginal increment analysis: W_b, width of the last band; W_{b-1}, penultimate band width. Inner layer radius = 362 µm.

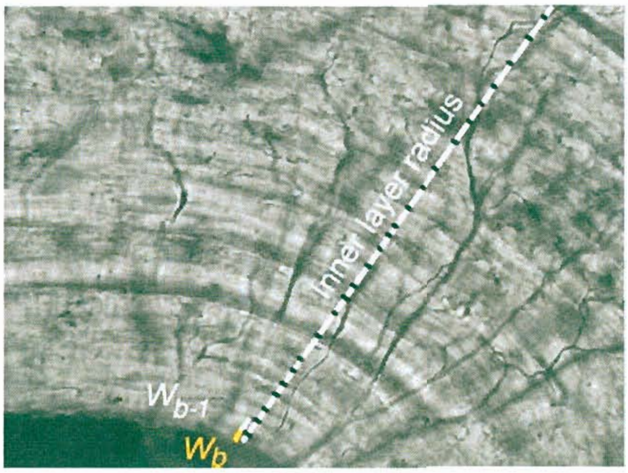
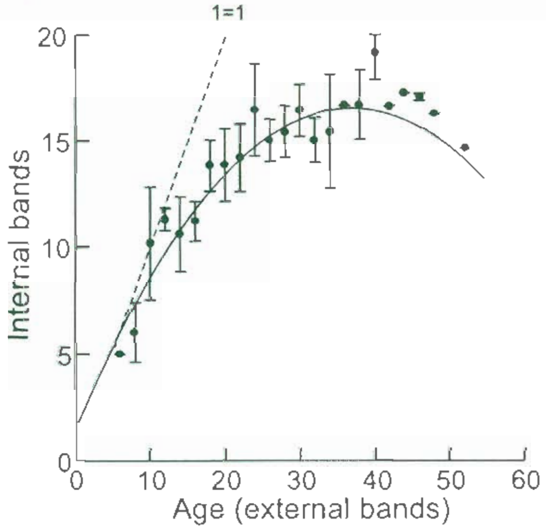


Fig. 7. Relationship between external bands (EB) and internal bands (IB). Plots are means, and error bars represent ±1 standard error. The polynomial relationship was $IB = -0.011(EB^2) + 0.813(EB) + 1.552$ ($r^2 = 0.918$, $n = 111$). Broken line indicates the exponential relationship if 1 EB = 1 IB.



reading precision (CV > 20%). A readability score of 2 was the most common. Near-term embryos had poor inner spine structure, and no bands were found in the dentine layers of embryos, making birth-band subtractions unnecessary.

The reparameterized VBGM was fitted to internal spine age data (Fig. 5*b*; the parameters are listed in Table 1). The Francis parameters indicated that females grew faster than males. Males grew 20 cm between the formation of 10 internal bands (between bands 2 and 12) compared with 40 cm for females. Over the next 10 bands (12 to 22 bands), males only grew by 1 cm compared with 6 cm for females.

Kimura's test found a strong difference between the L_∞ of each sex ($p < 0.001$), whereas there was only a slight difference between the k parameters of each sex ($p = 0.034$).

The number of internal bands (ages) ranged from 0 to 27 for females and from 0 to 22 for males. Most of the females collected had 8–16 internal bands, whereas males with 10–16 internal bands were more commonly collected.

Correlation between external and internal growth bands

A strong curvilinear relationship ($r^2 = 0.936$) was found between the number of external and internal bands (Fig. 7), with the number of external bands exceeding internal bands in most samples. The polynomial relationship showed that the first five bands were deposited at the same rate. However, over the next 10 years (external band ages 5 to 15), only one internal band was deposited for every 1.25 external bands. After 15 years, this rate rapidly declined, and after the age of 30, no new internal bands were deposited.

The growth curves from external bands were significantly different to the growth curves from internal bands. Francis parameters greatly differed for males, and Kimura's likelihood ratio test calculated a difference in the VBGM k parameter for each sex (male $p = 0.023$; female $p = 0.015$), whereas L_∞ also differed between the curves for males ($p = 0.007$).

Verification

The inner dentine layer of samples collected in spring had more wide opaque marginal edges than other edges (Fig. 8*a*), although a trend of annual band deposition could not be confirmed $\chi^2_3 = 1.32$ (NS). A high mean MI ratio was calculated for each season (Fig. 8*b*), and MI did not differ significantly between seasons (ANOVA, df = 3, $F = 0.744$, $p = 0.538$). The small number of readable spine sections with 16–19 bands ($n = 30$) limited the use of marginal increment analysis, and both edge and marginal increment analyses failed to confirm a distinct seasonal pattern in band deposition.

The radiometric ages presented in Fenton (2001) were similar to the external band age estimates from this study (Fig. 9). There was no significant difference between the length-at-age data from external bands and radiometric age data from vertebrae (ANOVA, $p = 0.31$, $F = 1.07$).

Longevity

Based on the maximum number of external bands (A_{max}), female *C. crepidater* live about 20 years longer than males; the oldest male examined was 34 years old and oldest female was 54 years old.

Age at maturity

External band counts indicate that females mature (A_{50}) at about 20 years (SE = 0.5) (Fig. 10); this is 37% of A_{max}. Maturity occurred over a very broad age range (12–42 years), although the youngest female in the early stages of pregnancy (fertilised eggs in utero) was 27 years old, whereas the youngest pregnant female with near-term embryos was 29 years old.

Females matured over a wider age range than males. External band counts indicate that male maturity occurred over an 8-year period, the youngest mature male was 9 years old, and the oldest immature male was 17 years old. Male A_{50} was estimated to occur at the age of ~9 years (SE = 1.4) (Fig. 10), which is 26% of A_{max}.

Discussion

Dorsal spines affect the hydrodynamics of the dorsal fin and offer a degree of protection from predation (Maisey 1979). *Centroselachus crepidater* embryos have fully formed spines, although most of the spine is beneath the skin. After birth, external spine growth is rapid. A smaller external spine in utero may reduce the risk of injury to both mother and siblings, whereas a larger spine after birth may have a defensive and locomotory function.

Growth increments

The relationship between animal length and spine length suggests that *C. crepidater* spines continue to grow throughout life, making them a suitable structure for estimating age and investigating growth. Internal bands, similar to those reported by Tanaka (1990), were found in spine cross sections. However, external bands proved to be an alternative (and probably more accurate) method to estimate age.

Fig. 8. (*a*) Proportion of edge type (solid diamonds, translucent; open squares, wide opaque; solid circles, narrow opaque) per season for both sexes combined. (*b*) Mean seasonal marginal increment (±1 standard error) for the inner dentine layer of *Centroselachus crepidater* second dorsal-fin spines with 16–19 opaque zones (n = 30).

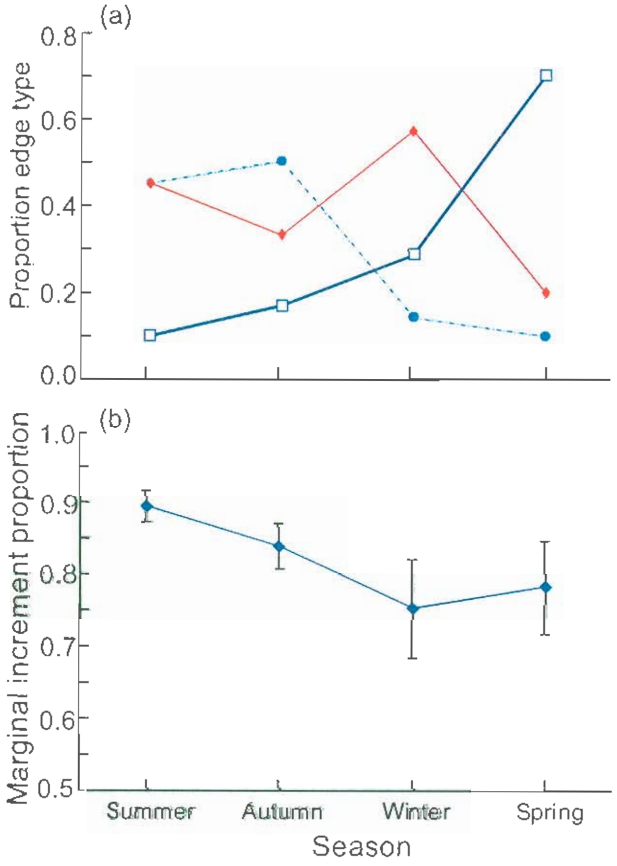


Fig. 9. Reparameterized von Bertalanffy growth curve generated from external spine data (solid circles) for female *Centroselachus crepidater* from southern Australia. Absolute age (×) from Fenton (2001), error bars represent error from radiometric technique. Growth curve generated from internal spine data (broken line) is included for comparison.

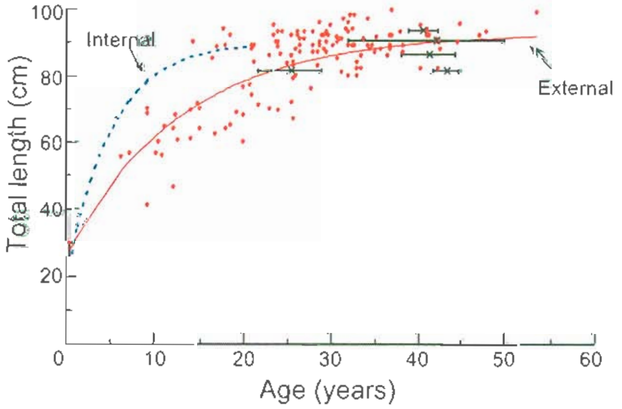
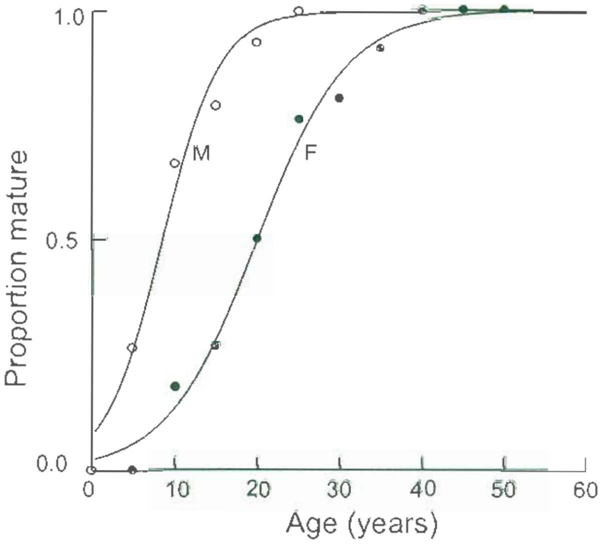


Fig. 10. Age at maturity ogives based on external band data for *Centroselachus crepidater* from southeastern Australia: male (M, open circles), n = 84, $P_{\mathrm{A}} = 1/(1 + e^{(-\ln(19)(\mathrm{AGE}-8.7)/(15.0-8.7))})$, $r^2 = 0.99$; female (F, solid circles), n = 137, $P_{\mathrm{A}} = 1/(1 + e^{(-\ln(19)(\mathrm{AGE}-19.8)/(35.9-19.8))})$, $r^2 = 0.99$.



Holden and Meadows (1962) overlooked the external bands on *S. acanthias* spines because of the ease of counting enamel bands. Maisey (1979) examined the structure and function of selachian fin spines and reported faint growth lines at the spine base of squalid (*Squalus*, *Etmopterus*, and *Deania* species) and heterodontid spines. External bands have also been noted on the spines of *Centroscymnus owstoni*, *Centrophorus uyato*, *Centrophorus squamosus*, *Deania calcea*, *Deania quadrispinosa*, *Etmopterus baxteri*, *Etmopterus* sp. B (Last and Stevens 1994), *Etmopterus lucifer*, *Etmopterus pusillus*, *Oxynotus bruniensis*, *Proscymnodon plunketi*, *Squalus megalops*, and *Heterodontus portusjacksoni* from southeastern Australia (S. Irvine, personal observation). These observations suggest that external bands on the spine may be suitable for ageing numerous shark species, and their usefulness in estimating age should be examined in future age and growth studies. Staining may not be necessary or beneficial for some spines (e.g., alizarin red only superficially stains *Deania calcea* spines and this stain decreased the band readability; S. Irvine, personal observation).

Both internal and external bands increased in number with animal length, although most spines had more external bands. The relationship between internal and external counts suggests that bands only formed at the same rate in the first 5 years. Internal band formation dramatically declined after 20 external bands had formed, and internal bands cease to form after 30 years (based on external bands). Maisey (1979) could not find a venous return system in adult spines and suggested that the inside of adult spines stop growing when the space above the pulp cavity has been filled by dentine. As spine growth rate slowed, the inner bands became more narrowly spaced in larger and (or) older animals. External bands also become more tightly packed, and larger and (or) older animals had spine bases with very little dentine. However, the number of external bands did not affect spine readability or reading precision.

Soldat (1982) and Nammack et al. (1985) used different growth areas of the spine to investigate the age of *S. acanthias* from the Northwest Atlantic. Soldat counted the internal bands in spine cross sections and obtained maximum ages of 20 (males) and 26 (females) years, while Nammack et al. used the enamel cap bands and reported maximum ages of 35 (males) and 40 (females) years. Nammack et al. suggested that the difference might be due to internal bands being grouped together as annuli during counting by Soldat. However, the growth curves predicted by these studies are remarkably similar, and internal and external bands were counted at a similar rate until 20 internal bands; internal bands then ceased to form at the same rate as external bands. Beamish and McFarlane (1985) validated the periodicity of enamel cap bands on *S. acanthias* from the Northeast Pacific through mark and recapture with tetracycline injection. A tetracycline mark was observed on the enamel, at the spine base, and within the inner dentine layer, and it was assumed that internal dentine bands were also annual. However, this assumption requires verification across all age and size ranges, as internal bands may not form annually in spines of older *S. acanthias*.

Precision and verification

The precision of the age data as indicated by the CV values showed that external bands were easier to interpret than internal bands. External bands form because of the lack of synchrony in upward spine growth and the continuous production of dentine at the spine base. Investigating the periodicity of external bands was not attempted (by either edge or marginal increment analyses), as external bands are not deposited in the typical opaque or translucent band pattern. However, enamel and internal dentine bands may be suitable for either edge or marginal increment analysis.

Marginal increment analysis was attempted on spines with 16–19 internal bands. Guallart Furio (1998) suggested that increment analysis would be impossible on squalid spines, as obtaining sections from the same spine location is required. To ensure spine sections from a similar location were used for increment analysis, the diameter of the spine section and the inner layer radius were measured. Marginal increment analysis was attempted on the internal bands, although the periodicity of band formation was inconclusive because of the small number of animals collected in the appropriate age class each month or season. The high longevity of this species and the wide age range suggests that a very large ($n > 1400$) sample size would be required to accurately attempt either edge or marginal increment analysis on a single age class of *C. crepidater*. Verifying band periodicity in spines using marginal increment analysis or edge analysis is likely to remain problematic, especially when the study species have a high longevity or when samples are collected opportunistically over a limited sampling period.

The applicability of independent ageing techniques (including radiometric analysis and radiobomb carbon dating) on the dorsal-fin spine also deserves further attention. External spine age estimates for female *C. crepidater* were comparable with the absolute ages of five large females estimated by radiometric analysis from vertebrae (Fenton 2001). The results of Fenton (2001) are based on many assumptions, and Welden et al. (1987) suggested that elasmobranch vertebrae were unsuitable for radiometric analysis. However, the similarity between the two data sets indicated that further research into radiometric ageing of shark vertebrae is required.

McFarlane and Beamish (1987) reported the incorporation of tetracycline into *S. acanthias* spines, making them a suitable structure to age after chemical tagging. However, very little is known about the survivability rate or chance of recapture of deepwater sharks. Yano and Tanaka (1986) successfully tagged and tracked two deepwater dogfishes (*Centrophorus acus*) caught by dropline, although this tracking study was abandoned after 24 h. Deepwater sharks may therefore survive being brought to surface waters to allow conventional tagging and tetracycline injection for ageing purposes.

Growth

The cue for growth (and therefore band deposition) in the deep sea is unknown. An annual cycle in food quantity and quality is often assumed (Clarke 2000; Swan and Gordon 2001), although seasonal dietary changes have not been investigated for deepwater dogfishes. Off southern Tasmania, there is no seasonal change in the species composition for the more abundant species, although micronekton composition does vary seasonally (Williams and Koslow 1997). This suggests that, if a change in diet is the cue for growth, it may be an increase in prey abundance (quantity) rather than a change in prey species (quality).

The Francis (1988) reparameterized von Bertalanffy growth model fits the observed length-at-age data well. Male and female growth was similar until males became mature. Males matured (A_{50}) at about 9 years, whereas females matured at about 20 years. However, maturity analysis required samples to be put into age classes represented by their lower values; age at maturity may therefore best be indicated over an age range.

Maturity

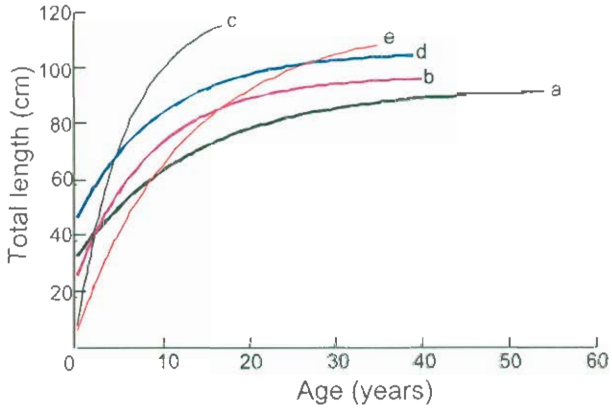
The estimated age at maturity differed from the age at maternity (the youngest pregnant female). Females matured at about 20 years, although the age of youngest female with candled uteri (early pregnancy) was 27 years and the age of the youngest female with near-term embryos was 29 years. Walker (2004) suggested the use of a maternity ogive rather than a maturity ogive for estimating recruitment in population dynamic models.

However, this becomes difficult for species that have an unknown gestation period and resting stage between pregnancies. There is no difference in the size at maturity (L_{50}) and the size of the smallest pregnant female (both 82 cm TL) (S. Irvine, unpublished data), suggesting that females might not grow during reproductive activity. Further growth may only occur during the resting period (between pregnancy and next follicle development phase).

Productivity

Centroselachus crepidater from southeastern Australia exhibits slower growth (Fig. 11) and higher longevity than most other dogfish species. However, *C. squamosus* from the Northeast Atlantic has a longevity of 70 years (Clarke et al.

Fig. 11. Various von Bertalanffy growth curves for female dogfish species: a, *Centroselachus crepidater*, this study; b, *Squalus acanthias*, Nammack et al. (1985); c, *Centrophorus acus*, Tanaka (1990); d, *Centrophorus granulosus*, Guallart Furio (1998); e, *Deania calcea*, Clarke et al. (2002*b*).



2002*a*) and remains the oldest dogfish species ever aged (albeit unvalidated).

Centroselachus crepidater from southeastern Australia has a mean litter size of six and the reproductive cycle is noncontinuous with no seasonal trend (Daley et al. 2002). Although the length of gestation is unknown, it seems reasonable to assume that the reproductive cycle (follicle development and gestation and resting period) would exceed 1 year and is probably 2 or more years. If a cycle of 2 years were assumed, an annual fecundity of three would indicate a maximum productivity of 102 offspring per lifetime. However, if the cycle were 3 years, then the maximum productivity would only be 68 offspring per lifetime.

The resilience of a species to fishing pressure depends on vulnerability to the fishing gear and biological productivity (Stevens et al. 2000). The high longevity and late age at maturity of *C. crepidater* from southeastern Australia are indicators of low productivity. Smith et al. (1998) assessed the productivity of 26 shark species using published age at maturity and maximum reproductive age data. According to this rank of sensitivity to fishing pressure, *C. crepidater* has a lower recovery capability than all of the Pacific shark species examined by Smith et al.

Nonselective trawl fishing off southeastern Australia collected a wide age range of *C. crepidater*, although most females had only recently matured (24–34 years old). The removal of this crucial component is likely to be unsustainable, and precautionary management regimes (including closed areas) need to be implemented immediately to avoid local extirpations. In light of this new information on age and growth, international management and conservation attention need to be directed towards dogfishes.

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SPECIAL ISSUE SKATES

Dietary comparisons of six skate species (Rajidae) in south-eastern Australian waters

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Abstract The diet of six skate species caught as bycatch in south-eastern Australian waters was examined over a 2-year period. The skates were segregated into two regions (continental shelf and continental slope) based on prey species and depth of capture. The shelf group consisted of four species, *Dipturus* sp. A, *D. cerva, D. lemprieri* and *D. whitleyi*, while the slope group comprised two species, *Dipturus* sp. *B* and *D. gudgeri.* The two groups varied in feeding strategies with the shelf species generally occupying a broader feeding niche and preying on a larger diversity of prey including a variety of crustaceans (brachyurans, anomurans, achelates, carideans and dendobranchiates), cephalopods, elasmobranchs and teleosts. Within the slope group, *Dipturus* sp. B and *D. gudgeri* were more specialised. *Dipturus* sp. B preyed primarily on anomurans (galatheids) and bachyurans (homolids), whereas *D. gudgeri* preyed primarily on teleosts. A size related change in diet was evident for all species with the exception of *D. gudgeri* in which all sizes preyed predominantly on teleosts. Smaller representatives of the four shelf species all preyed on numerous amounts of caridean shrimps, in particular *Leptochela sydniensis*. In contrast, the continental slope species, *Dipturus* sp. B consumed anomurans when small, shifting to brachyurans with increasing size. Of the six skate species examined in this study, three were secondary consumers (trophic level <3) and the remaining three tertiary consumers (trophic level >4). Although ANOSIM found significant differences in dietary composition between species within groups, there was some overlap in prey species amongst co-existing skates, which suggests that there is some degree of resource partitioning amongst them.

Keywords Trophic level · *Dipturus* · Prey · Niche · Partitioning

Introduction

Skates (Rajiformes) are a frequent bycatch in the southeast Australian trawl (Wayte et al. 2006), drop-line (Daley et al. 2006) and gillnet fishery (Walker et al. 2006). They are regarded as a low value by-product and are mostly discarded. However, as a result of their abundance and wide distribution they constitute a substantial percentage of the benthic community (Graham

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et al. 2001). At least 12 species of skates occur in the benthic habitat of southeast Australia (Last and Stevens 1994). The benthic habitat where these skates reside is poorly understood with only limited ecological studies on the demersal fish communities of the area. Therefore, our understanding of trophic interactions and relationships in the region are equally poorly documented (Bulman et al. 2001), and especially so with the skates.

Despite skates (Rajiformes) containing about 245 described species world-wide (Ebert and Compagno 2007) and being caught regularly as bycatch of demersal fisheries (Bonfil 1994), they are poorly studied in comparison to other elasmobranchs (Orlov 1998). Few studies exist on the comparative feeding ecology of four or more sympatric skate species in the one location (Ebert et al. 1991; Ellis et al. 1996; Orlov 1998, 2003; Dolgov 2005; Fariasa et al. 2006) and less information on trophic levels and their placement within food webs (Morato et al. 2003; Braccini and Perez 2005). Results from these comparative feeding studies have shown that some competition can occur between skate species and other benthic organisms and that a high biomass of skates in an area can have a significant impact on the benthic fauna.

Total reported landings of skates (excluding the animals that are either misidentified or classified under the generic ‘rays’) from the southeast trawl fishery have increased from 30 tonnes in 1992 to 46 tonnes in 2002 (Treloar unpublished data). This data suggests that skates are being landed in increasing quantities and it is therefore necessary to determine trophic levels to gain an insight into the impact catches may have on the trophic ecology of the demersal community. Given the lack of dietary information on the southeast Australian skate assemblage this study provides the first information on the comparative feeding ecology and trophic levels of six skate species in south-eastern Australian waters. The species considered in this paper include *Dipturus* sp. A [sensu Last and Stevens 1994 = *Raja* sp. A], *Dipturus* sp. B [sensu Last and Stevens 1994 = *Raja* sp. B], *Dipturus cerva, Dipturus gudgeri, Dipturus* (*Dentiraja*) *lemprieri* [Last and Yearsley 2002] and *Dipturus* (*Spiniraja*) *whitleyi* [Last and Yearsley 2002].

Methods

Study area and sample collection

From March 2002 to June 2004, six skate species (*Dipturus* sp. A, *Dipturus* sp. B, *D. cerva*, *D. gudgeri*, *D. lemprieri*, and *D. whitleyi*) were collected from commercial and scientific vessels operating in south-eastern Australian waters (Fig. 1). Samples were collected from fishers operating (24 h operation) demersal trawls (18–700 m), Danish-seines (20–64 m), gill nets (5–20 m) and bottom drop-lines (300–585 m).

Skates were identified using Last and Stevens (1994), sexed, weighed (nearest gram) and the total length (TL) measured (nearest 1.0 mm). Stomachs were excised and their contents weighed (nearest gram) and preserved in 70% ethanol for subsequent examination. Stomach fullness was assessed using a visually estimated scale of 1–5 (1, empty; 2, 0–25% full; 3, 26–50% full; 4, 51–75% full; 5, 76–100% full). Level of digestion was assessed using a visual ranking scale where: 1 = prey items that were only slightly digested and easily distinguishable; 2 = medium level of digestion, prey items distinguishable; and 3 = an advanced level of digestion, prey items not easily distinguishable. Prey items assigned to a level 3 were largely unidentifiable and excluded from further analysis. Prey items were identified to the lowest possible taxon using various identification guides (Hale 1927–1929; Gomon et al. 1994; Jones and Morgan 1994; Edgar 2000; Poore 2004) and each individual item weighed (wet) using an analytical balance (±0.0001 g). A collection of otoliths extracted from known species was used to identify fish fragments that were otherwise unrecognisable (Furlani et al. 2007). Prey items such as hydroids, algae, salps and sponges were considered to be incidentally ingested and were not included in diet analysis. Parasitic nematodes were excluded from the analysis.

Dietary analyses

Prey items were sorted into 11 major categories to facilitate dietary comparisons: Dendobranchiates (prawns), carideans (shrimp), brachyurans (crabs), isopods, achelates (crayfish and pill-

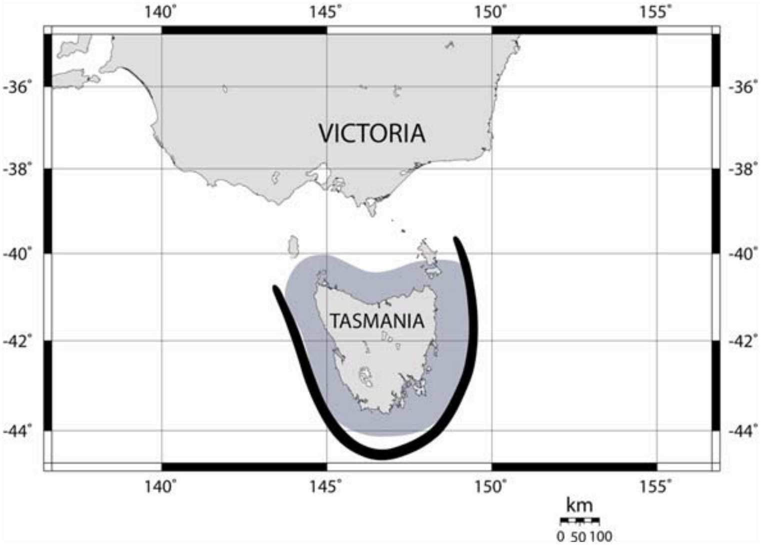

Fig. 1 Skate sample collection sites from south-eastern Australian waters. *Dipturus* sp. A, *D. cerva, D. lemprieri* and *D. whitleyi* () occurring in waters along the continental shelf and *Dipturus* sp. B and *D. gudgeri* (■) occurring along the continental slope

bugs), anomurans (squat lobsters), cephalopods (octopus and squid), molluscs (gastropods and bivalves), teleosts (fish excluding Anguilliformes), Anguilliformes (eels), and elasmobranchs (sharks, skates and rays). Where fewer than four higher taxa items were identified (in total) from all stomachs, these were excluded from further analysis (Moura et al. 2005). The importance of prey was assessed using several indices to avoid the bias inherent in each (Cortés 1997).

Percentage Frequency of Occurrence $\%F = \frac{N_i}{N_s} * 100$ where N_i is the number of individuals containing dietary category i and N_s is the total number of stomachs examined (Hyslop 1980).

Percentage Mass $\%M = \frac{W_i}{W_{sc}} * 100$ where W_i is the total weight of prey category i taken from all skates and W_{sc} is the total weight of all prey from all skates, and

Percentage Number $\%N = \frac{N_i}{N_{sc}} * 100$ where N_i is the total number of prey category i taken from all skates and N_{sc} is the total number of all prey from all skates (Hyslop 1980).

Comparisons among species were carried out using the Percentage Index of Relative importance (%IRI):

$$\%\mathrm{IRI} = \frac{100\,\mathrm{IRI}}{\sum_{i=1}^{n}\mathrm{IRI}}$$ (Cortés 1997) where

$\mathrm{IRI} = (\%N + \%M) * \%F$ (Pinkas et al. 1971) and $\%N$ and $\%M$ are defined above.

Some authors (MacDonald and Green 1983; Hansson 1998) suggest that IRI values under represent lower taxonomic categories. We incorporate both IRI and the stomach fullness index, expressed as the product of the ratio of the mass/volume of a particular prey category in a stomach and the total mass/volume of all prey in that stomach (described later in the MDS analysis methods), to describe the difference in diet between species.

The mean %IRI contributions to the diet of skates of the top five prey categories (based on contribution by %IRI) were plotted against size class (Table 1) to provide a visual representation of ontogenetic changes in diet.

Preliminary multivariate analysis indicated that the dietary compositions of the females and males of all species were not statistically different ($P > 0.05$). In all subsequent analysis sexes have been pooled, this was also the case for spatial and temporal data.

To determine whether sufficient stomach samples were collected to characterise the diet for each species and size class, randomised cumulative prey curves were generated (Ferry and Cailliet 1996). Each skate was assigned a size class depending on species and sample size (Table 1). Prey species diversity was calculated using the pooled quadrat method based on the Brillouin Index of Diversity (Pielou 1966; Braccini

Table 1 Size classes (cm) of all skate species for data analysis

*Dipturus*sp. A		*Dipturus* sp. B		*D. cerva*		*D. gudgeri*		*D. lemprieri*		*D. whitleyi*	
<45	(47)	<82	(16)	<45	(40)	<75	(15)	<45	(21)	<75	(17)
45–55	(90)	>83	(17)	45–55	(78)	76–100	(34)	>46	(42)	76–100	(13)
>56	(109)			>56	(25)	>101	(20)			>101	(16)

Sample sizes in parentheses

et al. 2005). Stomach samples of each size class in each species were randomised (×100) and re-sampled with replacement to calculate cumulative mean diversity and standard deviation (Koen Alonso et al. 2001). When the curve reached an asymptote, the number of stomachs was considered sufficient for accurately describing the diet.

The trophic level of skates was calculated using the trophic index (TR):

$$\mathrm{TR} = 1 + \left(\sum_{j=1}^{n} P_j * \mathrm{TR}_j\right) \quad \text{(Cortés 1999)}$$

where TR_j is the trophic level of each prey taxa j and P_j is the proportion of each prey taxa in the diet of a skate species, based on %IRI values (Braccini and Perez 2005). A list of trophic levels of prey categories ($n = 8$) from the lowest taxonomic level was taken from various sources (Pauly et al. 1998a; Cortés 1999; University of Columbia 2005). Unidentified crustaceans were excluded from this analysis. Cluster analysis was performed in PRIMER v5.2.2 (Clarke and Gorley 2001) to determine similarities in trophic levels between the six skate species.

Niche breadth was quantified using Levins' Index (B): $B = 1/\sum p_j^2$ (Levins 1968) where p_j is the fraction by weight of prey items in the diet of food category $j(\sum p_j = 1)$. Niche breadth was calculated using 20 prey categories (see Table 3). Because few teleosts were identified to species or family level they were placed into one category. A lower index indicated a narrow niche breadth (Ellis et al. 1996).

Non-metric multi-dimensional scaling ordination (MDS) using the PRIMER v5.2.2 (Clarke and Gorley 2001) was used to examine changes in diet with respect to size (Table 1). Primer was also used for size comparisons across species with size classes standardised to <50 cm TL, 51–100 cm TL, and >101 cm TL. The data used for this analysis follows the methods of Linke et al. (2001) and White et al. (2004) in which the Stomach Fullness Index is expressed as the product of the ratio of the mass/volume of a particular prey category in a stomach and the total mass/volume of all prey in that stomach. In most instances, the mean of a random sub-sample (Table 2) of these values (based on the desired analysis categories e.g. size, etc) were square root transformed and subjected to MDS using a Bray–Curtis similarity matrix (White et al. 2004).

One-way analyses of similarities (ANOSIM) were used to determine if prey categories differed significantly amongst skate species or sizes and whether any paired relationships existed. Similarity percentages (SIMPER) were used to identify significantly important dietary categories. Multivariate dispersion (MVDISP) was used to determine the amount of dispersion within one group of points, i.e. species (White et al. 2004).

Results

Diet comparison

Depth segregation occurred among the six skate species, with two distinct groups being present. *Dipturus* sp. B and *D. gudgeri* (frequently caught by bottom drop-liners) occurred in depths of 300–

Table 2 The number by which each species was pooled for size comparisons

	Dipturus sp. A	*Dipturus* sp. B	D. cerva	*D. lemprieri*	*D. gudgeri*	*D. whitleyi*
Size	24	4	12	6	8	4

700 m, whereas *Dipturus* sp. A, *D. cerva, D. lemprieri* and *D. whitleyi* were caught in depths ranging from 1 to 280 m. Cumulative prey curves were constructed for each species by size class and showed either well-defined asymptotes or trends towards an asymptote (Fig. 2). This indicated that sufficient stomachs were examined to describe the diet for most size classes and species.

Thirty-six species, 37 genera, and 36 families of prey items were identified in the six skate species examined (Table 3). The most diverse taxa were crustaceans (containing 17 families and over 19 identified species); amongst which brachyurans were the most numerous infraorder, followed by carideans. Teleosts were of importance to two species with Anguilliformes being consumed by five of the six skate species and Platycephalidae (flathead) occurring in the diet of three skate species. Juvenile elasmobranchs occurred in three of the six skate species examined.

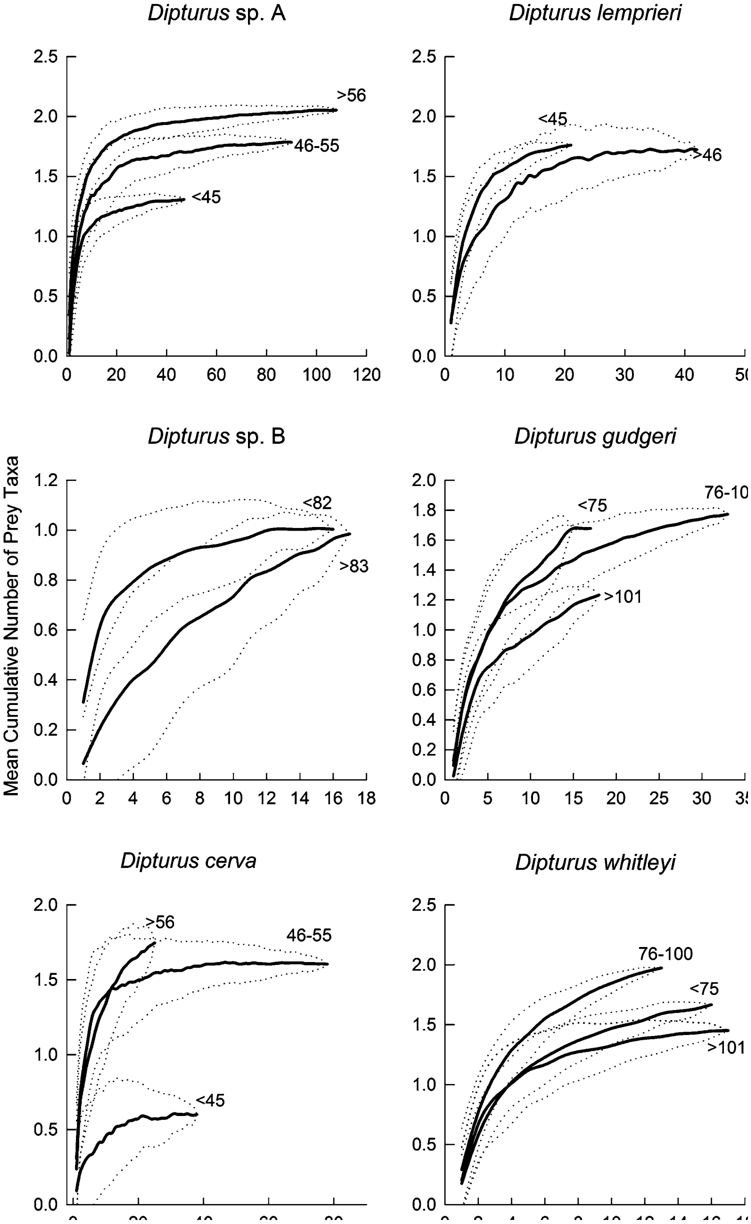

Fig. 2 Mean cumulative diversity of prey taxa plotted against cumulative number of stomach samples for all size classes (TL cm) in *Dipturus* sp. A, *Dipturus* sp. B, *D. cerva*, *D. gudgeri*, *D. lemprieri* and *D. whitleyi*. Dotted line indicates ± 1 SD

Table 3 Diet composition of six skate species in terms of frequency of occurrence (%*F*), contribution by number (%*N*), mass (%*M*) and index of relative importance on a percent basis (%IRI) for the major prey taxa and identifiable dietary categories

Major taxa	*Dipturus* sp. A				*Dipturus* sp. B				*D. cerva*				*D. gudgeri*				*D. lemprieri*				*D. whitleyi*			
	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI
Mollusca		**10.2**	**26.3**	**23.9**						**2.4**	**1.8**	**0.9**		**2.3**	**0.2**	**0.1**		**3.2**	**5.0**	**0.0**		**8.4**	**27.0**	**27.7**
Cephlapoda[a]	20.8	10.0	26.1	23.9					13.3	2.4	1.8	0.9	3.2	2.3	0.2	0.1	13.2	3.2	5.0	0.0	23.6	7.9	26.9	27.7
Gastropoda[a]	0.5	0.2	0.2	0.0																	1.8	0.5	0.1	0.0
Crustacea		**78.0**	**27.2**	**56.8**		**96.4**	**90.2**	**98.9**		**95.3**	**86.5**	**97.4**		**58.7**	**21.8**	**19.7**		**91.0**	**75.7**	**89.7**		**73.3**	**29.5**	**32.0**
Callapidae[a]	15.7	25.0	2.5	13.7					48.8	59.7	12.6	65.7	3.2	9.0	0.7	0.5	18.4	16.2	1.7	9.3	10.9	27.2	0.2	11.2
Cancridae[a]	2.2	1.8	0.5	0.2					5.4	0.6	2.5	0.1					6.6	1.6	2.6	0.3				
Caridea[a]	0.5	0.4	0.1	0.0					3.0	1.6	1.2	0.2												
Dendobranchiata[aa]	3.4	3.9	1.1	0.5	34.1	55.5	15.7	37.8	24.1	12.9	39.0	20.4	19.4	16.9	5.2	6.9	17.1	13.3	30.7	21.1	3.6	2.0	0.1	0.3
Galatheidae[a]					2.3	0.7	0.3	0.0	3.6	0.5	0.4	0.1												
Goneplacidae[a]	0.3	0.1	0.3	0.0					1.2	0.1	1.1	0.0									3.6	1.0	5.0	0.8
Homolidae[a]	0.3	0.1	0.1	0.0																	1.8	3.5	2.5	0.4
Hymenosomatidae[a]	2.9	1.2	1.2	0.2					1.2	0.1	0.3	0.0					15.8	9.2	16.1	11.2	1.8	0.5	0.1	0.0
Isopoda[a]	1.7	0.8	0.8	0.1	9.1	10.7	2.5	1.9	5.5	1.1	2.5	0.4					2.6	4.3	2.8	0.5				
Leucosidae[a]					40.9	21.0	70.1	58.0					15.1	10.2	14.0	5.9					1.8	0.5	1.7	0.2
Majidae[a]	0.7	2.1	0.2	0.1													1.3	0.3	0.0	0.0				
Palinuridae[a]	12.0	10.7	4.9	6.0					0.6	0.1	0.0	0.0					11.8	7.2	3.4	3.5	3.6	1.5	0.2	0.1
Pilumnidae[a]	0.3	0.1	0.2	0.0	4.6	1.4	0.7	0.1	0.6	0.1	1.3	0.0									1.8	0.5	1.5	0.1
Portunidae[a]	0.3	0.1	0.1	0.0																				
Raninidae[a]	8.8	7.6	5.1	3.6					10.8	6.3	11.0	3.9					14.5	14.2	3.5	5.7	9.1	15.4	6.9	3.8
Scyllaridae[a]																					1.8	1.5	0.5	0.0
Unidentifiable	29.7	24.2	10.1	32.3	13.6	7.1	1.0	1.1	35.5	12.1	14.6	6.5	16.1	22.6	1.9	6.4	55.3	24.7	14.9	38.1	20.0	19.8	10.8	15.0
Elasmobranchs[a]		**0.1**	**0.2**	**0.0**						**0.5**	**2.3**	**0.1**						**0.3**	**0.6**	**0.0**		**0.5**	**1.1**	**0.1**
Scyliorhinidae	0.3	0.1	0.2	0.0					2.4	0.4	1.9	0.1												
Rajidae									0.6	0.1	0.2	0.0												
Urolophidae									0.6	0.1	0.3	0.0					1.3	0.3	0.6	0.0	1.8	0.5	1.1	0.1
Teleosts[a]		**11.7**	**46.3**	**19.3**		**3.5**	**9.8**	**1.0**		**2.0**	**9.1**	**1.6**		**39.1**	**78.0**	**80.3**		**5.6**	**18.4**	**10.3**		**17.8**	**42.4**	**40.2**
Anguillidae	6.9	3.8	4.3	1.8					6.0	1.0	1.9	0.4	3.2	4.5	1.4	0.3	1.3	0.3	0.0	0.0	9.1	3.5	4.3	2.7
Antennariidae	0.5	0.2	2.7	0.0																				
Bythitidae																					1.8	1.0	0.4	0.1
Callionymidae									0.6	0.1	0.0	0.0									1.8	1.0	2.2	0.2
Gempylidae																					1.8	1.0	5.9	0.5
Macrouridae					2.3	0.7	5.4	0.2					1.1	0.8	1.0	0.0								
Moridae																					1.8	0.5	4.0	0.3
Pegasidae	0.3	0.2	0.2	0.0																				
Platycephalidae	1.7	0.7	7.2	0.4													2.6	0.9	2.9	0.3	1.8	1.0	1.9	0.2
Pleuronectidae	0.3	0.1	0.6	0.0																				
Sebastidae																					1.8	0.5	1.2	0.1
Syngnathidae																					1.8	0.5	0.5	0.1
Triglidae	1.0	0.3	6.8	0.2													1.3	0.4	0.3	0.0				

Table 3 continued

Major taxa	*Dipturus* sp. A				*Dipturus* sp. B				*D. cerva*				*D. gudgeri*				*D. lemprieri*				*D. whitleyi*			
	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI	%*F*	%*N*	%*M*	%IRI
Unidentifiable	17.2	6.5	24.5	16.9	6.8	2.8	4.4	0.8	7.2	0.9	7.2	1.2	45.2	33.8	75.6	79.9	18.4	4.0	15.2	9.9	30.9	8.9	22.1	36.0
Total no. of stomachs	410.0				113.0				166.0				263.0				77.0				60.0			
No. of stomachs containing food[b]	335.0				37.0				160.0				72.0				72.0				48.0			
Percentage of stomachs containing food	81.7				33.0				96.4				27.4				93.5				80.0			
Mean stomach fullness	2.7				1.9				2.9				1.9				2.9				2.8			
Niche breadth (*B*)	4.1				1.7				3.7				2.2				3.8				4.1			

[a] Prey categories for Niche Breadth analysis

[b] This excluded stomachs containing 100% unidentified digested matter

A total of 410 *Dipturus* sp. A stomachs were examined, 75 of which were empty (Table 3). A wide variety of prey was consumed with crustaceans representing the largest proportions (%*N*) and diversity (%*O*). Brachyurans contributed the most to this subphylum, consisting of at least eight families. Carideans were of secondary importance (14% IRI) in this subphylum with *Leptochela sydniensis* dominating (13% IRI). Cephalopods were also important (24% IRI), occurring in 22% of stomachs. Teleosts occurred in 21% of stomachs and contributed the most in mass (46%). Other prey categories such as Elasmobranchs, Dendobranchiata, Achelata, Anomura, Isopoda and Gastropoda were of lesser importance. The importance of each prey category changed with the increase of skate size and ANOSIM values indicated that dietary composition differed among size classes ($P < 0.001$; global *R* statistic 0.78) (Fig. 3). Dendobranchiata/carideans (50%) and brachyurans (44%) dominated the diet of small individuals (<45 cm TL), whereas teleosts (46%), brachyurans (30%) and cephalopods (24%) were of more importance in the larger size classes (>56 cm TL).

One hundred and thirteen *Dipturus* sp. B stomachs were examined, of which 76 were empty (Table 3). *Dipturus* sp. B had the least diverse diet of all six skate species. Crustaceans (99% IRI) were the most important taxa, with brachyurans predominantly *Dagnaudus petterdi* (Homolidae) dominating the diet. Galatheids (anomurans) were second most important, occurring in 34% of stomachs. Very few teleosts occurred in the stomachs examined (1% IRI). ANOSIM showed that there were significant differences in dietary composition among size classes ($P < 0.03$; global *R* statistic 0.79) (Fig. 3). Although brachyurans were the predominant prey found in *Diptrurus* sp. B, small skates (<82 cm TL) consumed large amounts of anomurans and small amounts of brachyurans and teleosts (Fig. 3). A change in diet occurred with the larger skates (>83 cm TL) consuming predominantly brachyurans.

A total of 166 *D. cerva* stomachs were examined, six of which were empty (Table 3). The diet of *D. cerva* consisted of predominantly crustaceans with carideans (66%), primarily *L. sydniensis* being of greatest importance. Brachyurans

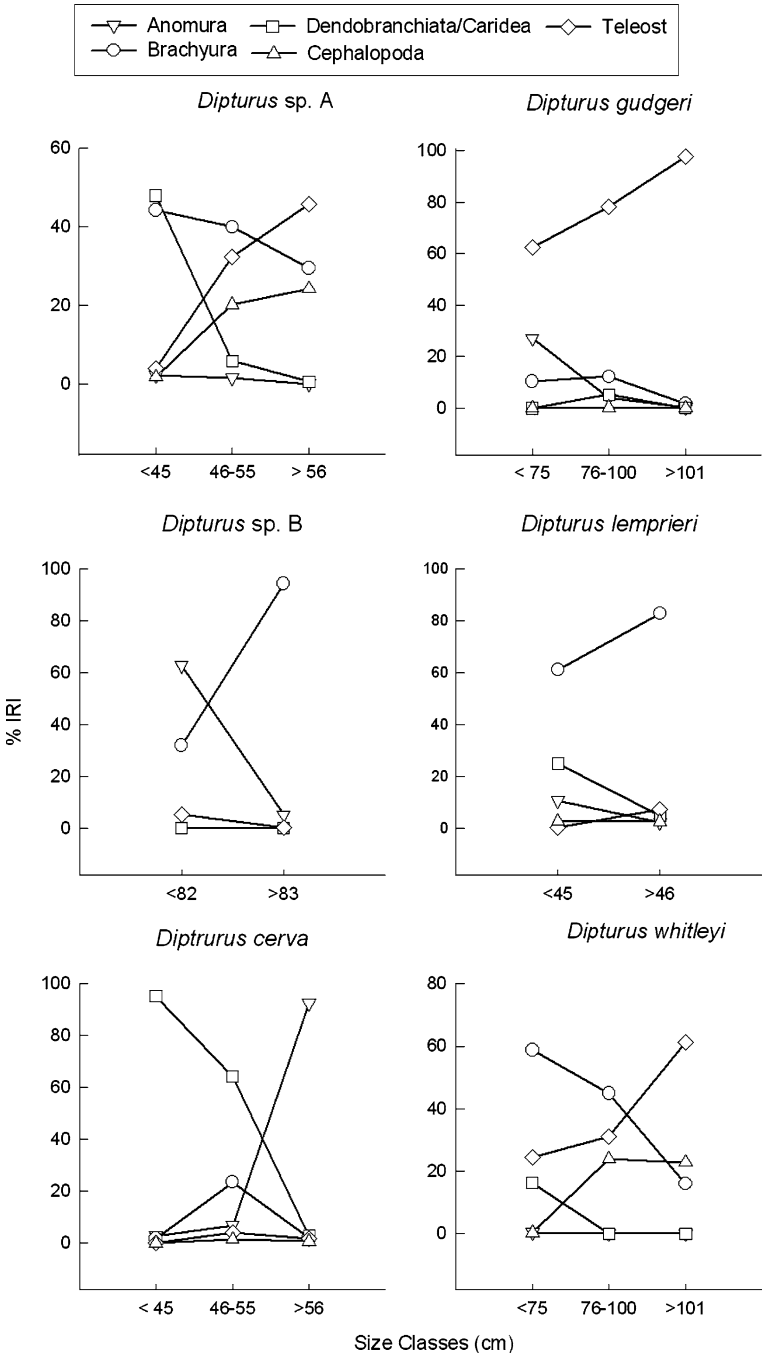

Fig. 3 Percentage of IRI by size class for the six skate species

consisted of at least five families occurring in 29% of stomachs, whereas anomurans occurred in 24% of stomachs but contributed the most by mass (39%). Teleosts, elasmobranchs, dendobranchiates, achelates, cephalopods and isopods were of lesser importance to the diet of *D. cerva.* Although elasmobranchs were of lesser importance, a diverse range of taxa occurred in the diet including *Asymbolus* spp. (including egg cases), rajids and urolophids (Table 3). All prey items varied in level of importance throughout size classes (Fig. 3), which was reflected in the ANO-

SIM analysis ($P < 0.001$; global R statistic 0.67) suggesting significant differences between size classes. Dendobranchiates/carideans were dominant in two size classes (<45 and 46–56 cm TL) but decreased in importance as the skate increased in size, whereas brachyurans and teleosts started to become of more importance in the 46–56 cm TL size class. Anomurans dominated the diet of individuals >56 cm TL.

A total of 263 *D. gudgeri* stomachs were analysed, of which 191 of these were empty (Table 3). *Dipturus gudgeri* consumed a narrow range of prey species with teleosts dominating the diet. Most teleosts could not be identified, with the exception of two families, Anguillidae and Macrouridae. Brachyurans, predominantly *D. petterdi* (6% IRI) and anomurans (7% IRI), were of less importance. ANOSIM showed no changes in diet across size classes ($P > 0.05$; R statistic 0.14) although anomurans were of more significance in small individuals (<75 cm TL) and teleosts increased in %IRI with size but still dominated all size classes (Fig. 3). Brachyurans (Homolidae) and dendobranchiates/carideans were less important in all size classes.

Stomachs were collected from 77 *D. lemprieri*, of which five were empty (Table 3). The diet of *D. lemprieri* consisted of a wide range of prey items with crustaceans dominating the diet. Brachyurans were the most dominant infraorder with five families identified in 74% of the stomachs, although the majority of the brachyurans were unidentified. Anomurans were important in the diet of *D. lemprieri* in terms of %IRI and contributed the most in mass. Carideans, cephalopods, isopods, elasmobranchs, and teleosts were of less importance. ANOSIM showed significant differences in diet among size classes ($P < 0.04$; global R statistic 0.22) (Fig. 3). Dendobranchiates/carideans were of some importance in small individuals (<45 cm TL), although brachyurans dominated this size class and increased in importance with increasing size (>46 cm TL). Cephalopods, teleosts and anomurans were of little importance.

Sixty *D. whitleyi* stomachs were examined, 12 of these were empty (Table 3). The diet of *D. whitleyi* was the most diverse out of all six skate species. Teleosts contributed the most in terms of %IRI and mass. *Dipturus whitleyi* consumed the greatest diversity of teleosts of all the skate species consisting of at least eight families, although 36% by IRI were still unidentified. The majority of these teleosts were benthic; however two benthopelagic species (Gemiphylidae spp.) were identified. Anguilliformes were only present in 9% of the stomachs, although they occurred most in the diet of this species. Cephalopods, primarily *Octopus* spp. occurred in 24% of stomachs contributing 28% (IRI), whereas brachyurans (including unidentified) occurred in 36% of stomachs contributing 19% in terms of percentage IRI. Carideans, anomurans, achelates, elasmobranchs and gastropods were of lesser importance. ANOSIM showed that diet differed amongst size classes ($P < 0.03$; global R statistic 0.28) with brachyurans dominating both the <75 cm TL and 76–100 cm TL size classes but becoming of less importance as the skate increased in size (Fig. 3). Cephalopods became more important in the 76–100 cm TL size class and teleosts became increasingly important from 76 cm TL onwards (Fig. 3). Dendobranchiates/carideans were of little importance throughout all size classes.

Skate trophic levels

Skate trophic levels ranged from 3.6 in *Dipturus* sp. B to 4.2 in *Dipturus* sp. A and *D. whitleyi*. Fish, eels, elasmobranchs, and octopus had the highest trophic levels and therefore contributed the most to species that consumed these prey groups (Table 4). All skate species that had a TR of <4.0, fed primarily on crustaceans, whereas the diet of *D. gudgeri* and *D. whitleyi* (TR >4.0) consisted primarily of teleosts, and several elasmobranchs, crustaceans, and octopus. *Dipturus* sp. A fed on a mixture of these.

Cluster analysis identified two distinct TR groupings within the six skate species (Fig. 4). The greatest similarity was found between *Dipturus* sp. A and *D. whitleyi*, which both largely preyed on fish and octopus. The second group included *Dipturus* sp. B and *D. lemprieri* which targeted primarily crustaceans (Fig. 4; Table 4).

Table 4 Standardised trophic compositions and trophic levels of six skate species

Species	Fish (3.2)	Eels (4.2)	Squid (3.2)	Octo (3.8)	Crabs (2.6)	Sh/Pr (2.7)	Crus (2.5)	Elasmo (4.1)	TR
Dipturus sp. A	0.22	0.02	–	0.30	0.27	0.18	0.01	0.00	4.2
Dipturus sp. B	0.00	–	–	–	0.60	0.00	0.39	–	3.6
D. cerva	0.01	0.00	0.00	0.01	0.07	0.71	0.22	0.00	3.7
D. gudgeri	0.85	0.00	0.00	0.00	0.06	0.00	0.07	–	4.1
D. lemprieri	0.12	0.00	–	0.02	0.40	0.13	0.25	0.08	3.8
D. whitleyi	0.37	0.03	–	0.28	0.19	0.11	0.01	0.00	4.2

Prey taxa are abbreviated as follows: (Octo = octopus; Sh/Pr = Shrimps/Prawns; Crus = Other Crustacea (i.e. anomurans, isopods, etc); and Elasmo = Elasmobranchs). Trophic levels for each prey group are in parentheses

Comparisons of feeding habits

Ordination of the %*M* contributions for the two deep-sea skate species (*Dipturus* sp. B and *D. gudgeri*) identified significant differences ($P = 0.001$; global R statistic 0.68, Fig. 5A). SIMPER demonstrated that brachyurans and teleosts were responsible for this difference. Niche breadth differed between the two species with *Dipturus* sp. B (1.7) having a lower niche breadth than *D. gudgeri* (2.2) (Table 3). ANOSIM demonstrated no significant difference between size classes (Fig. 5B).

Ordination using percentage mass contributions suggested prey overlap for the shelf species *Dipturus* sp. A, *D. cerva, D. lemprieri* and *D. whitleyi* (Fig. 6A). However ANOSIM ($P < 0.001$; global R statistic 0.34) suggested otherwise finding significant differences among all species. These differences were reflected by the MDVSIP values which showed *Dipturus* sp. A had the lowest dispersion (0.82) and *D. whitleyi* had the highest dispersion value (1.28). Pair-wise comparisons suggested that differences were greatest between *D. cerva* and *D. whitleyi* ($P < 0.001$; R statistic 0.52). SIMPER identified

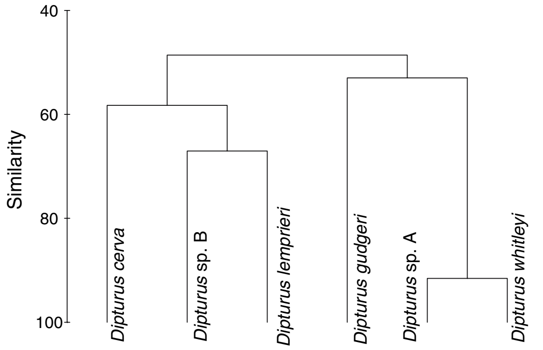

Fig. 4 Cluster analysis of the similarities in the dietary composition contributing towards trophic levels for six skate species

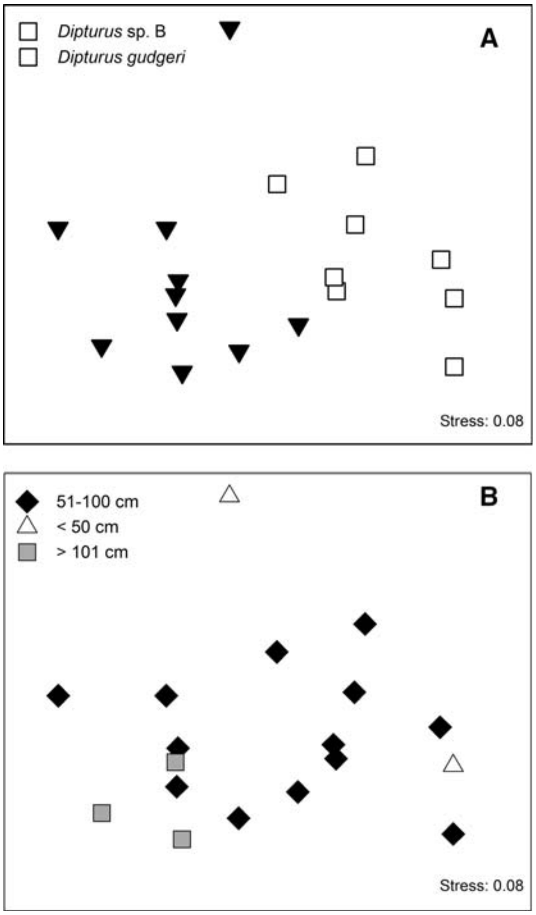

Fig. 5 (**A**) Non-parametric MDS ordination of mean percentage mass contributions for *Dipturus* sp. B and *D. gudgeri.* (**B**) Non-parametric MDS ordination of mean percentage mass contributions for *Dipturus* sp. B and *D. gudgeri* size classes)

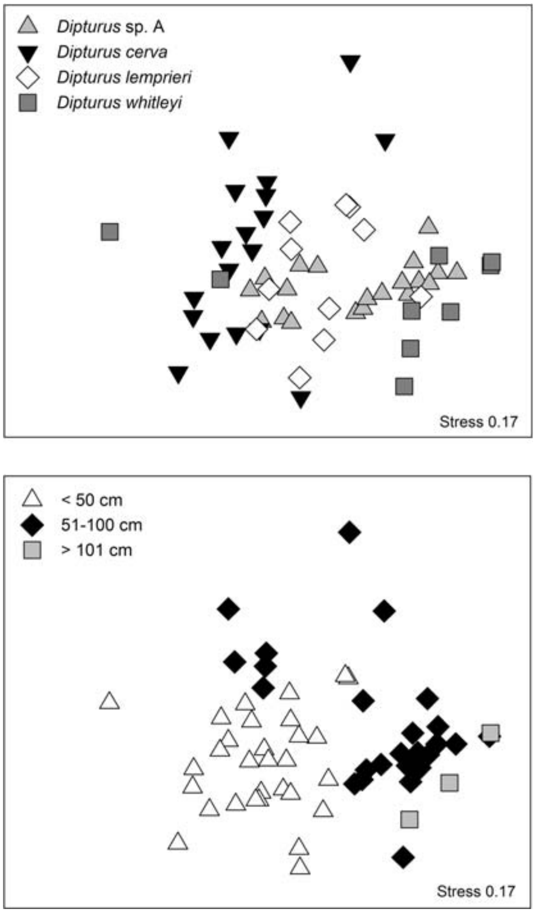

Fig. 6 (**A**) Non-parametric MDS ordination of mean percentage mass contributions for *Dipturus* sp. A, *D. cerva*, *D. lemprieri* and *D. whitleyi.* (**B**) Non-parametric MDS ordination of mean percentage mass contributions for *Dipturus* sp. A, *D. cerva*, *D. lemprieri* and *D. whitleyi* size classes

carideans as the prey item responsible for this separation. *Dipturus cerva* and *D. whitleyi* had the smallest and largest niche breadth, respectively (Table 3). MDS showed significant differences among the three size classes of all skate species (Fig. 6B).

Discussion

The six skate species studied here can be broadly divided into two groups based on different prey species and depth preferences. *Dipturus* sp. B and *D. gudgeri* occurred along the continental slope, whereas *Dipturus* sp. A, *D. cerva, D. lemprieri* and *D. whitleyi* were common on the continental shelf, as was also observed by Last and Stevens (1994). Segregations of skate species has also been observed off the west coast of southern Africa where Ebert et al. (1991) found that 14 species were separated by depth zones. The fishing methods used to sample skates in this study were similarly divided between these depth zones with mostly droplines and some trawling occurring on the continental slope and Danish seine, trawling and gillnetting occurring on the shelf. This poses some difficulties in the interpretation of these data as past studies have shown that gear selectivity affects catch composition (Walker 2004) and can bias fish dietary studies (Morato et al. 2003). In the context of this study, biases were identified in stomach fullness data and our ability to identify prey species (from areas not sampled in this study). Both *Dipturus* sp. B and *D. gudgeri* were primarily collected by baited demersal dropline and both frequently had empty stomachs or contained only bait and/or hooks. Studies have shown that fishes feeding to satiation have a reduced response to bait (Lokkeborg et al. 1995), thus fishes with empty stomachs are more likely to be caught and form a disproportionate percentage of the catch. A high occurrence of empty stomachs has also been reported in other elasmobranch dietary studies using baited long-lines as a collection method (Morato et al. 2003; Lokkeborg et al. 1995).

A diverse range of prey species were found among the six skate species, with some species having greater prey diversity than others. Remarkable differences were detected between the two assemblages, with the shelf species having a more diverse diet than the slope species. In contrast, Ebert et al. (1991) found the South African slope species consumed a higher diversity of prey than the shallower shelf species. Niche breadth can give an indication of whether a species is a generalist or specialist feeder (Levins 1968). The continental slope species *Dipturus* sp. B and *D. gudgeri* both had low niche breadths (≤2.2), suggesting they may be specialist feeders but this study did not determine the range of potential prey available nor sample the populations widely (Gerking 1994), thus conclusions are difficult to draw.

Within the area studied *Dipturus* sp. B was found to be a crustacean specialist, preying mostly on *Dagnaudus petterdi* (antlered crab), and galatheids (squat lobsters). In contrast, the sympatric species *D. gudgeri*, a large skate attaining 185 cm TL predominantly targeted teleosts, at least one (*Lepidorhynchus denticulatus*) of which was benthopelagic. Different predator strategies are required to target these very different prey groups, the latter requiring more mobility and the former a capacity to crush robust exoskeletons. The large size of *D. gudgeri* is likely an advantage in preying on teleosts as it enhances the species capacity to move or potentially herd prey. Factors such as mobility, seasonal occurrence, abundance and distribution of potential prey, as well as ecomorphology, which are known to effect diet (Smale and Cowley 1992; Muto et al. 2001; Motta 2004) have not been assessed here.

Niche breadth (3.7–4.1) for the four continental shelf species indicated that they were more generalised feeders, but as is the case with the deeper water representatives studied here, it is unclear if this is a result of prey targeting or if it just represents the diversity of available prey species. The diet of *D. cerva* and *D. lemprieri* consisted almost exclusively of benthic crustaceans. *Dipturus cerva* largely targeted small, soft bodied crustaceans such as shrimp, *L. sydniensis*, while *D. lemprieri* was more opportunistic targeting a wider diversity of benthic crustaceans but predominantly brachyurans. Teleosts and cephalopods were sporadically preyed on by *D. lemprieri* suggesting a more opportunistic predatory behaviour. The diet of *D. lemprieri* was similar to *Dipturus* sp. A which also consumed benthic crustaceans, although other prey items including octopus and benthic teleosts were of greater importance in the latter species. The broader niche breadth of *Dipturus* sp. A suggests that this species is potentially more mobile or has a different foraging strategy providing greater opportunity to prey on more mobile organisms. *Dipturus whitleyi* had the most diverse diet of all shelf skates targeting a variety of crustaceans, octopus and teleosts. This emphasises the opportunistic nature of the feeding strategies employed by this species, and is likely a function of its large size in comparison to the other shelf skates examined here, being born at ~20 cm TL (Last and Stevens 1994) and attaining 200 cm TL. The four continental shelf skate species studied here targeted similar prey, but consumed different proportions of each, suggesting there is niche specialisation and separation amongst them.

Interestingly, the four shelf species preyed on small quantities of elasmobranch egg cases and juveniles which may be due to their similar spatial distributions. Studies have shown that embryos of egg-laying elasmobranchs are susceptible to predation (Cox and Koob 1993) because of the signal given off by the embryo circulating water around the egg case, this signal can be detected by the mechanoreceptive lateral line of certain predators (Luer and Gilbert 1985; Collin and Whitehead 2004). Skates have been documented to feed on juvenile elasmobranchs in other parts of the world, although they did not contribute significantly to the overall diet (Ebert et al. 1991; Smale and Cowley 1992; Orlov 1998; San Martin et al. 2007).

Intra-specific size-related changes in diet

Although ontogenetic changes occurred in all species examined in this study with the exception of *D. gudgeri*; cumulative prey curves for some size classes (*D. cerva* >56 cm TL, *D. gudgeri* >101 cm TL, *Dipturus* sp. B >83 cm TL, and *D. whitleyi* <75 cm and 76–100 cm TL) did not reach an asymptote. Consequently, more stomachs for these size classes may be needed to adequately describe the diet. Small benthic crustaceans were consumed in all species at smaller sizes but variations amongst them became more evident with increasing size. Some species made a transition to larger crustaceans with more robust exoskeletons (*Dipturus* sp. B, *D. cerva* and *D. lemprieri*), whereas others consumed larger proportions or larger teleosts (*Dipturus* sp. A, *D. whitleyi* and *D. gudgeri*). The small benthic shrimp *L. sydniensis* made up a large proportion of the diet of small individuals but only occurred in the shelf skate species as it does not occur in deeper waters (Poore 2004). The smaller continental slope species *Dipturus* sp. B preyed on small galatheids initially, an observation also noted in skate species in other parts of the world (Koen Alonso et al. 2001). Unquantified observations during this study indicated that juvenile skates have less developed teeth and smaller mouths than adults and it is unlikely that they have the ability to crush harder and large prey. The results of this study support those of Smale and Cowley (1992) and Fariasa et al. (2006) who found a relationship between predator body and mouth size and changes in diet to larger prey. The implications of these results are that prey species are potentially more a function of size rather than other life history characteristics. However, all factors (including tooth morphology between the species) were not thoroughly investigated in this study.

The diet of the continental slope skate *D. gudgeri*, unlike the other skates examined here, did not change from one prey group to another with increasing size, rather it remained feeding exclusively on teleosts with these increasing in proportion and size with increasing skate size. Similar patterns have been observed in other skate species where teleosts dominate the diet (Lucifora et al. 2000). This behaviour has been identified mostly in large skates where they are able to exploit a broader habitat range and capture larger more mobile prey items to meet their energetic requirements (Muto et al. 2001). This was further demonstrated in this study by the large shelf skate *D. whitleyi* which also preyed on teleosts throughout all size classes. Several bentho-pelagic prey species were found only in the diet of these two larger species (*D. gudgeri* and *D. whitleyi*). Studies have reported pelagic species such as anchovies, *Engraulis capensis*, and pilchards, *Sardinops ocellatus*, in the diet of skates (Ebert et al. 1991; Smale and Cowley 1992) but a lack of understanding of the spatial and temporal distribution of potential prey species makes drawing conclusions difficult. For example, pelagic prey may be targeted only when near the sea floor rather than skates feeding pelagically.

Trophic levels

Surprisingly few studies have focused on skate trophic levels and their placement within the food web (Morato et al. 2003; Braccini and Perez 2005). The diet information gained from this study has demonstrated that both the continental slope and shelf skate species examined are secondary and tertiary consumers. The tertiary consumers (>4.0) preyed more widely on eels, other teleosts, octopus and elasmobranchs which contributed high energy/trophic levels between 3.2 and 4.2. Similar results were found for the thornback ray, *Raja clavata*, in the northeastern Atlantic Ocean which had a TR of 4.1 and consumed a large quantity of teleosts (Morato et al. 2003), whereas the diet of the sand skate, *Psammobatis extenta*, in Argentinean waters consisted primarily of small invertebrates, and had a TR of 3.5 (Braccini and Perez 2005).

Trophic levels identified in this study were sensitive to how the prey items were classified. For example, in the present study eels (Anguillidae) were separated from other teleosts. Teleosts alone exhibited a TR of 3.2, whereas eels had a significantly higher TR of 4.2. If eels are grouped with other teleosts, the TR is lowered, as Cortés (1999) also noted a more precise trophic level is calculated if each prey item is identified to the lowest taxon.

There have been several conflicting issues on what factors contribute to higher trophic levels (Pauly et al. 1998b; Cortés 1999). Cortés (1999) found a positive correlation between body size and trophic levels for some shark species, although there are exceptions in large sharks such as the basking shark (*Cetorhinus maximus*), megamouth shark (*Megachasma pelagios*), and the whale shark (*Rhincodon typus*), that are filter feeders primarily feeding on zooplankton. From this study, it was determined that *Dipturus* sp. A (attaining ~70 cm TL) and *D. whitleyi* had the highest trophic levels (TR = 4.2) suggesting that size may not be the major determining factor but rather the prey ingested. Cluster analysis demonstrated similarities between species that fed on similar prey and that had similar trophic levels.

Overlap amongst species

The two sympatric continental slope skate species (*Dipturus* sp. B and *D. gudgeri*) demonstrate little overlap in prey. It has been hypothesised by McEachran et al. (1976) that a more abundant and less specialised skate may reduce the diversity of prey of a less abundant and more specialised species by out-competing the less abundant species for its preferred prey. This scenario may also be applicable to *Dipturus* sp. B and *D. gudgeri* on the continental slope as the latter is larger, more abundant and widespread, therefore probably more dominant in this environment. Our data indicates that, despite *D. gudgeri* being larger than *Dipturus* sp. B, it is unlikely that size can solely account for differences in prey species found between these two skates.

The four sympatric continental shelf skate species examined in this study (*Dipturus* sp. A, *D. cerva, D. lemprieri* and *D. whitleyi*) had limited overlap in prey items indicating some partitioning of prey resources reducing potential competition. Our results suggest that partitioning of prey resources among the shelf species was largely a function of skate size, and that there was little overlap of prey among similar sizes. Similar results have been reported by Smale and Cowley (1992).

Conclusion

Prior to this study, little information existed on the feeding habits of the skate species in Tasmanian waters, south-eastern Australia. This work has provided fundamental information on the diet of two sympatric skate species (*Dipturus* sp. B and *D. gudgeri*) from the continental slope and four sympatric species (*Dipturus* sp. A, *D. cerva, D. lemprieri* and *D. whitleyi*) from the continental shelf region. The species in these two assemblages showed variations in feeding strategies that exploited different food sources.

The slope assemblage consisted of specialised feeders, with *Dipturus* sp. B targeting anomurans and a particular species of brachyuran, whereas the diet of *D. gudgeri* consisted almost exclusively of teleosts. This feeding strategy could be influenced by less abundant and less diverse food resources in the deeper environment (Laptikhovsky 2005), or abundances of one species out competing the other. Although spatial and seasonal factors may greatly contribute to resource partitioning there are no indications of seasonal variability in fish diet on the continental slope (Bulman et al. 2002) and food has been recognised as the commonly partitioned resource in marine fish environments (Ross 1986).

Within the shelf species, the prey groups exploited were diverse comprising of crustaceans (carideans, achelates, anomurans, brachyurans and isopods), octopus, elasmobranchs and teleosts. Limited prey items were shared amongst the species suggesting partitioning of prey resources with skate body size being a contributing factor. Resource partitioning among these species may also be due to their morphological attributes that have developed independently as a result of prey use and environmental conditions, allowing multiple species to utilise the similar habitat (Connell 1980).

To date, our understanding of these benthic ecosystems is scant. To increase knowledge of higher predators within this region further study into benthic communities is essential.

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Spatial and temporal variation in the reproductive biology of gummy shark *Mustelus antarcticus* (Chondrichthyes : Triakidae) harvested off southern Australia

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Abstract. *Mustelus antarcticus*, endemic to southern Australia, exhibits matrotrophic aplacental viviparity. Differences in synchronous ovarian and parturition cycles, mostly annual west and biennial east of longitude 138°E, are explained by environmental differences. Ovulation and parturition peak during November–December and the gestation period is ~12 months. Largest ovarian follicle diameter ranges from 15 to 28 mm at ovulation, and mean wet mass gain is 10-fold from *in utero* egg (~10 g) to full-term embryo (~100 g) at ~330 mm total length. The sex ratio of embryos *in utero* is 1:1, and litter size (1 to 57 embryos) rises curvilinearly with maternal length. Length-at-maternity and length-at-maturity increased with rising fishing mortality and subsequently decreased with falling fishing mortality. These patterns are explained by the hypothesis on the 'phenomenon of apparent change of size-at-maternity' (and size-at-maturity) caused by gill-net length-selective fishing mortality, which masks any potential density-dependent responses. Male length-at-maturity estimates from seminal vesicle condition, testis development and spermatogenesis stages are similar, but are less than estimates from clasper calcification. Maximum body mass of females is double that of males and, at any length >700 mm, mean body mass of females exceeds that of males.

Additional keywords: embryonic growth, fishery assessment, maternity, maturity, ovarian cycle, reproduction.

Introduction

The gummy shark (*Mustelus antarcticus*) is endemic to southern Australia, where the species is harvested by demersal fishing on the continental shelf and upper slope. The species occurs to depths of 350 m (Last and Stevens 1994), but 96% of the mass of gummy sharks captured during 2003–04 was taken at depths <80 m (Walker and Gason 2005).

The shark fishery off southern Australia began targeting *Galeorhinus galeus* using baited hooks attached to bottom-set longlines in Bass Strait during the mid-1920s. Bottom-set monofilament gill-nets of mesh-size 150 to 200 mm were introduced into the fishery during the mid-1960s and, by the early 1970s, most of the catch was taken by this method. At that time, 7-inch (178-mm) and 8-inch (203-mm) mesh-sizes were variously adopted, whereas at present there is a legal minimum mesh-size of 6 inches (152 mm) and a legal maximum mesh-size of 6.5 inches (165 mm). After adoption of gill-nets, *M. antarcticus* gradually replaced *G. galeus* as the predominant species in the catch (Walker 1999; Walker and Gason 2005). Stock assessment age-structured production models indicate that *M. antarcticus* stocks have been markedly reduced, but are harvested sustainably at a level close to the maximum sustainable yield (Walker 1994, 1998; Pribac *et al.* 2005). In contrast, the *G. galeus* stocks have been severely depleted (Punt and Walker 1998; Punt *et al.* 2000), but catches of the other significant byproduct species (*Pristiophorus cirratus*, *P. nudipinnis* and *Callorhinchus milii*) are considered sustainable.

Any population analysis, whether it is fishery stock assessment, demographic analysis associated with ecological risk assessment, or assessment for risk of species extinction, requires the same specific parameters for three components of reproduction. These are sex ratio at birth, the litter-size-maternal-length relationship, and the relationship of the proportion of the female population in maternal condition (contributing to the next annual recruitment) expressed as a function of length of shark (maternity ogive). Determination of the maternity ogive requires information on the periodicity of each of the ovarian cycle, gestation and parturition before the values of its parameters can be estimated. For fishery assessment, maturity ogives for females and males are also required if the management objectives for a fishery are expressed in terms of mature population number or mature biomass. An explicit definition of maturity is essential for this purpose (Walker 2005).

The present study was designed to address three objectives related to estimation of the required reproductive parameters and their spatial and temporal variation for *M. antarcticus* from data collected during three periods (1973–76, 1986–87 and 1998–01) between the Western Australia-South Australia and Victoria-New South Wales borders (Fig. 1). These objectives were: (1) Determine the reproductive parameters required for

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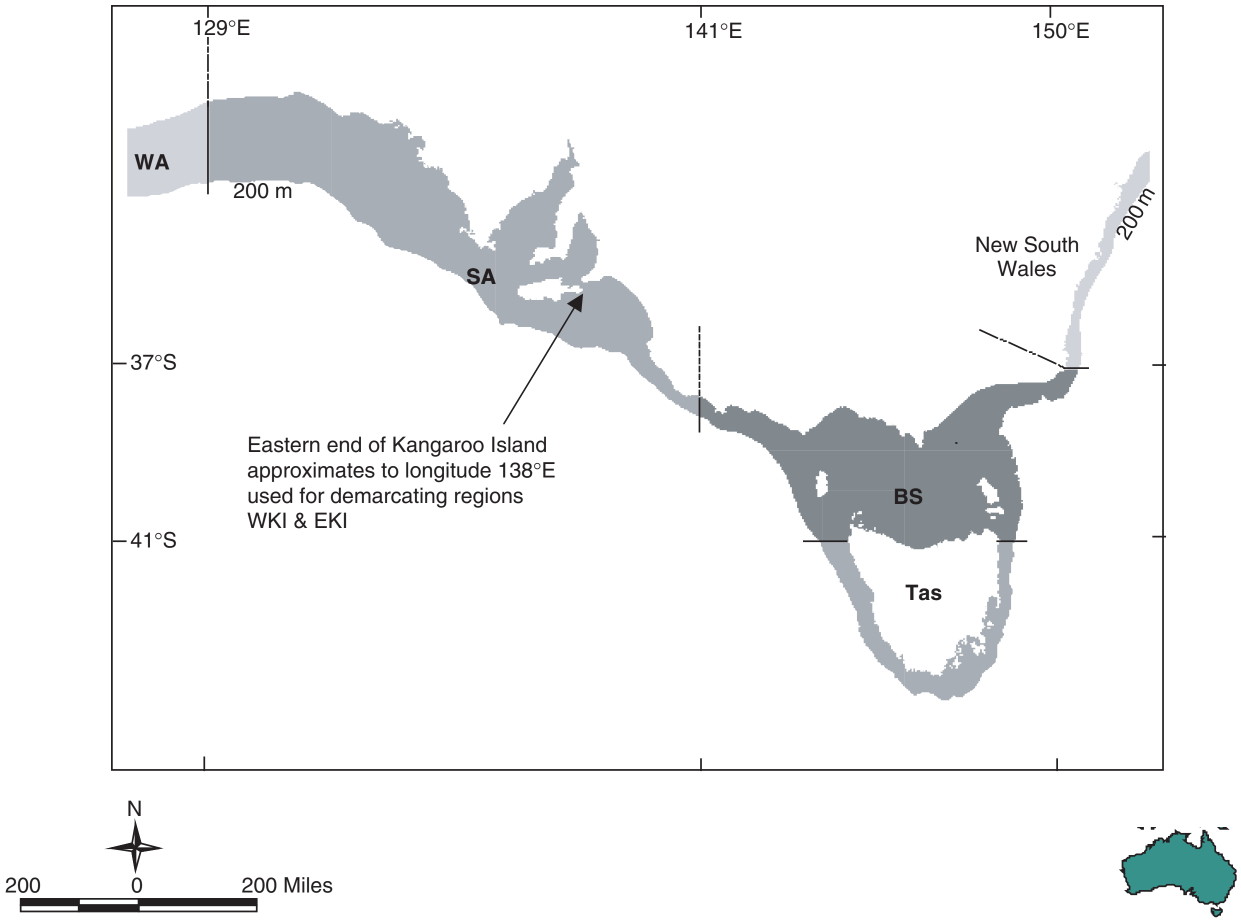

Fig. 1. Definition of adopted regions for *Mustelus antarcticus*. WA, Western Australia; SA, South Australia; BS, Bass Strait; Tas, Tasmania; WKI, West of Kangaroo Island; EKI, east of Kangaroo Island.

population analysis. (2) Determine whether the reproductive parameters have changed in response to a major increase in fishing mortality between 1973–76 and 1986–87, and a subsequent decrease between 1986–87 and 1998–01. (3) Determine whether the parameters vary between the two broad regions west and east of longitude 138°E (eastern end of Kangaroo Island). Initially, the third objective was to consider the two regions of Bass Strait and waters off South Australia, but the boundaries of the regions were altered for data analysis. Between 1973 and 1976, most sampling was undertaken in Bass Strait, where two-thirds of the all-time catch of *M. antarcticus* was taken; in contrast, between 1986 and 1987, sampling was repeated in Bass Strait and extended to waters off South Australia. Opportunistic sampling was undertaken between 1998 and 2001 in both regions while studies of other species were being conducted. The results from the present study were compared with those from Western Australia, where there is a separately managed shark fishery that also harvests *M. antarcticus*. A separate study of *M. antarcticus* reproduction along the south coast of Western Australia (Lenanton *et al.* 1990) was undertaken between October 1985 and October 1986 aboard commercial shark fishing vessels operating from Albany and Esperance.

The present study of *M. antarcticus* closely followed an approach applied to *G. galeus* in a similar study. The present study also followed the explicit definitions of 'onset of maturity', 'pregnancy', 'maternity', 'parturition frequency', 'litter size' and 'ovarian cycle' and other terminology adopted for *G. galeus* (Walker 2005). To further establish appropriate terminology and to provide essential background information to support the conclusions drawn by the present study, I first provide a brief description of the reproductive system of *M. antarcticus*. Also provided is a rationale for the boundary of Kangaroo Island applied to spatial analysis.

Description of reproductive system of Mustelus antarcticus

Female chondrichthyan fishes typically have paired or single ovaries and paired reproductive tracts. Each tract is differentiated into a funnel-shaped ostium, anterior oviduct, oviducal gland with (in some species) an isthmus leading to the uterus, uterine sphincter and – common to the paired reproductive tracts – the urogenital sinus.

Mustelus antarcticus has only the right ovary, which is roughly tear-shaped and adnate to the anterior portion of the lymphomyeloid epigonal organ. Functions of the ovary include oogenesis (development of germ cells), accumulation of yolk in developing oocytes from the blood, and synthesis and secretion of hormones. The ovary in immature females consists of numerous small white follicles (~1 mm diameter), but with the onset of maturity oocytes within the follicles begin to grow (folliculogenesis) (~1 to 3 mm). They then acquire yellow colouration with the accumulation of yolk (vitellogenesis) (usually >3 mm) (personal observation). Many of the preovulatory follicles at various stages of enlargement degenerate through resorption of yolk from the oocytes to form corpora atretica. During sequential ovulation of a series of oocytes in a mature female, each ovulated oocyte (ovum) is released as the follicle wall collapses to form a corpus luteum. The ovum, moved by cilia, passes through the peritoneal cavity and then through the ostium that bifurcates into the left and right oviducts. The ovum moves through one of the oviducts to one of the paired oviducal glands, where fertilisation and encapsulation of the fertilised egg with egg jelly occurs (Hamlett 1999). Initially spherical, the fertilised egg is compressed into an ellipsoid shape and encapsulated in a brownish-yellow, transparent, flexible tertiary egg envelope, the free ends of which are pleated, and deposited in the uterus (personal observation). The egg is fertilised from sperm stored in the oviducal gland (Storrie 2004). Some eggs *in utero* fail to develop embryos (Hanchet 1988; Walker 2005, present study), which are referred to herein as ‘infertile eggs’.

Mustelus antarcticus exhibits aplacental viviparity with minimal histotrophy (Hamlett *et al*. 2005*a*) and hence retains the encapsulated egg and subsequent embryo with its yolk-sac during gestation. The uterine walls are thick, spongy and vascular during early gestation but, as gestation advances, they become thin, semi-transparent and further vascularised. Uterine compartments form from the periphery of the internal surface of the uterine wall (Waite 1902) by a series of reduplications of non-vascular mucous membrane. The reduplications extend across the lumen to the opposite wall in the closely related species *Mustelus lenticulatus* (Parker 1882), and the compartments distend with a colourless fluid to enclose each embryo separately (Günther 1870). The formation of uterine compartments is characteristic of species that develop yolk-sac placentae, but not of aplacental sharks (Schlernitzauer and Gilbert 1966). However, *M. antarcticus*, like *Hemitriakis japanica* (syn. *Galeorhinus japonicus*), *M. manazo* (Chen and Mizue 1973), and *Mustelus canis* (Ranzi 1932), is an example of a species that forms uterine compartments in an aplacental species.

As described for *M. manazo* (Teshima and Koga 1973), the external yolk-sac of *M. antarcticus* is large during the early embryonic stages but, as the embryo grows, the external yolk-sac becomes progressively smaller as the yolk is consumed (see ‘Results’). As parturition approaches, the contracted yolk-sac and the short stalk by which it is attached appear to be incorporated into the body of the embryo when the yolk is completely absorbed. The egg case membrane remains intact, and unfolds and stretches to accommodate the developing embryo and increasing amounts of enclosed clear fluid (personal observation). As the yolk is depleted, the embryo is nourished by uterine secretions (histotroph) (Storrie 2004) following a transition in embryonic nutrition from a lecithotrophic phase to a histotrophic phase.

Male chondrichthyan fishes typically have external paired claspers that extend from the posterior bases of the pelvic fins. As the males mature, the claspers calcify and each articulates freely at the base (basipterygium). The paired internal organs include the testes, genital ducts, Leydig gland and siphon sacs in sharks and chimaeras or alkaline gland in batoids. The paired genital ducts, which cover the elongate kidneys embedded in the dorsal abdominal wall, consist of the efferent ductules, epididymis, ductus deferens and ampulla ductus deferens, and are covered by the peritoneum. The paired elongate testes are each embedded in the anterior portion of a long irregular epigonal gland, which is a lymphomyeloid organ supporting the testis. The testis, packed with spherical spermatocysts, performs the functions of spermatogenesis (germ cell generation) and steroidogenesis (synthesis and secretion of steroid hormones). Spermatozoa occur throughout the lumena of the epididymis, ductus deferens and ampulla ductus deferens, along with secretions from the genital ducts and from the Leydig gland (Hamlett and Koob 1999). During copulation, seminal fluids stored in the paired ampullae ductus deferens is ejaculated via the urogenital sinus and the urogenital papilla, located in the cloaca, to the dorsal groove of each clasper. With one or both claspers inserted through the urogenital sinus and paired uterine sphincters into the uteri of a female, the seminal fluids are washed along the dorsal groove of each clasper by sea water and secretions propelled under hydrostatic pressure from the paired ventral subcutaneous siphon sacs (Gilbert and Heath 1972). In the following, the term seminal vesicle, which is applied widely to non-homologous structures throughout the animal kingdom, is adopted in preference to ampulla ductus deferens because of common usage.

Materials and methods

Boundaries of regions for statistical analysis

The study sampled a single genetic stock (Gardner and Ward 1998, 2002; MacDonald 1988) distributed on the continental shelf and slope between Bunbury in Western Australia and Eden in southern New South Wales. Tagging provides evidence that this population extends north to Jervis Bay (latitude 35°06′S), with one tagged individual traveling to northern Sydney (35°40′S) (Primary Industries Research Victoria, unpublished data).

Preliminary examination of the data indicated differences in the patterns of reproduction in female sharks between Bass Strait (BS) and waters off South Australia (SA) in 1986–87 and from west to east of longitude 138°E between 1998 and 2001. In BS, about half the largest-sized females were in maternal condition during all three sampling periods. In SA, all the largest-sized females were in maternal condition during 1986–87, but only about half were in maternal condition between 1998 and 2001. From 1998 to 2001, most of the SA data were collected from an area between longitudes 138°E and 141°E, contiguous with BS; few data came from this area between 1973 and 1976 or between 1986 and 1987. Hence, for the purpose of data analysis, the regions were redefined as west of Kangaroo Island (WKI) and east of Kangaroo Island (EKI). WKI is the SA region minus the area between longitudes 138°E and 141°E, whereas EKI is the combined regions of BS and Tasmania south of latitude 41°S (Tasmania) plus the area in SA between longitudes 138°E and 141°E (Fig. 1).

There is also a sound biogeographical reason for redefining the regions by a boundary at longitude 138°E. The southern region of Australia, from Cape Leeuwin in Western Australia to Cape Howe in Victoria, covers two coastal biogeographical provinces that become separated at approximately the location of Kangaroo Island. Waters of the transitional warm temperate Flindersian Province are west of Kangaroo Island and affected by the warming effects of the Leeuwin Current flowing from tropical regions south along the west coast of Western Australia. Much of this warm water spreads east through the Great Australian Bight under the influence of the west wind drift. Waters of the cold temperate Maugean Province are east of Kangaroo Island and more influenced by the colder waters from summer upwelling at the continental shelf near the South Australia-Victorian border and the Flinders Current, which flows north past western Tasmania and bifurcates west and east along the Victorian coast (Knox 1963; Kailola *et al.* 1993).

Capture of sharks

Specimens were collected during three separate periods (1973–76, 1986–87 and 1998–01) in BS and SA, and a further small sample was collected between 1973 and 1976 in Tasmania (off the eastern coast) (Fig. 1). From 8 June 1973 to 29 November 1976, sharks were captured at 162 sites, mainly in BS (126 sites), but also in Tasmania (20 sites) and SA (16 sites). Experimental fishing gear deployed from research vessels consisted of 12 gill-nets and 400 hooks attached to two longlines. Eight mesh-sizes of the 12 gill-nets, each 250 m long and ~1.7 m high, ranged from two to nine inches (51 to 229 mm) in steps of one inch (25 mm). Between 28 February 1986 and 9 December 1987, sharks were captured at 144 sites in BS (60 sites) and SA (84 sites). Experimental fishing gear deployed from fishing vessels operating under normal commercial conditions consisted of four gill-nets, each 500 m long and ~2.4 m high, of four mesh-sizes ranging from five to eight inches (127 to 203 mm) in steps of 1 inch. From 10 November 1998 to 22 February 2001, sharks were captured at 153 sites in BS (91 sites) and SA (62 sites). Fishing gear deployed from vessels operating under commercial fishing conditions consisted of standard gill-nets of 6-inch mesh-size in BS and 6.5-inch mesh-size in SA. Each gill-net was up to 4200 m long, 20 meshes deep and ~2.4 m deep (Walker *et al.* 2005).

Biological sampling

Except between 1973 and 1976, when many of the captured sharks were tagged and released, most specimens of *M. antarcticus* were dissected to investigate reproduction and other aspects of their biology. The total length (TL) of sharks was measured to the nearest millimetre: the tail of each shark was first allowed to take a natural position and the upper caudal lobe was then placed parallel to the body axis. Sex, TL, several reproductive indices, and, when sea conditions permitted (mostly on a research vessel during the period 1973–76), mass of total body, liver, ovary (in females) and left testis (in males) were recorded for each shark. For both females and males, hepatic somatic index (HSI) was computed as liver mass/total body mass and gonad somatic index (GSI) was computed as gonad mass/total body mass.

Females were dissected and macroscopically inspected at sea in order to investigate breeding condition (maturity, pregnancy and maternity), litter size, period of gestation, period of ovarian cycle and the growth of embryos. Records were made of the diameters of the three largest follicles and the presence of corpora atretica and corpora lutea in the ovary and, for pregnant sharks, the number of eggs and embryos in each uterus. In addition, the TL, sex, uterus (left or right), and mass (with and without yolk sac) of each embryo were recorded for most pregnant sharks. Three separate indices were adopted for recording the condition of the ovary, oviducal gland, and uteri from rapid macroscopic inspection (Table 1). Oviducal gland condition was recorded, but was not considered a reliable indicator of female breeding condition and is not presented in the results.

Males were dissected and macroscopically inspected to investigate maturity using three separate indices for recording the condition of seminal vesicles, development of testes and calcification of claspers (Table 1). The seminal vesicles were also recorded as being 0-, 1-, 2-, 3- or 4-quarters full with seminal fluids. The length of the left clasper was measured from its basipterygium to the distal end. A histological approach for determining male maturity was only adopted between 1973 and 1976. Two or three pieces of testis tissue (4 to 8 mm thick) were removed at sea by transverse section from the left testis, and stored temporarily in Bouin's solution. The Bouin's solution was renewed every 12 h for ~36 h and then replaced with 10% neutralised formalin for subsequent laboratory processing.

Laboratory processing

Testis tissue pieces were dehydrated by immersion in a series of alcohol solutions (80 to 100%), cleared in chloroform and embedded in blocks of paraffin wax. Transverse sections of the embedded testis tissue were cut with a microtome to a thickness of 2 to 3 μm and mounted on microscope slides. The sections were then stained by a process requiring serial treatment with various solutions of xylol, alcohol, Mayer's haemotoxylin and eosin (Luna 1968), and protected by coverslips attached with adhesive. In preparation for microscopic determination, a straight-line marker (transect) was attached to the mounted section. The marker passed over the germinal zone of the distolateral edge of the testis, across the diameter and through the central region of the tissue mount to the medial edge of the testis. Using an 18-stage system for describing spermatocyst development (Mellinger 1965) and using a binocular microscope set at 400× magnification, the number of spermatocysts at each stage in contact with one edge of the transect was counted and recorded. In addition, the minimum and maximum stage detected from viewing the whole section were recorded.

Total body mass and total length

The relationship between total body mass, w, and TL, l, was determined using the power function $w = aclb$, where a and b are parameters estimated by linear regression $\ln(w) = \ln(a) + b \ln(l)$ and c is a coefficient for correcting bias caused by natural logarithmic transformation (Beauchamp and Olson 1973). The relationship was considered separately for males, non-pregnant females ($U = 1, 2, 3$, or 6), pregnant females with eggs in utero ($U = 4$), and pregnant females with embryos in utero ($U = 5$). Relationships for these four sex-breeding conditions (SBC) were considered separately because females grow larger than males, and because it was suspected that pregnant females weigh more than non-pregnant females at any length. Analysis of covariance

Table 1. Indices adopted for staging reproductive condition

Criteria for classing mature and immature condition; uterus condition was adopted for classing maternal and non-maternal condition (adapted from Walker 2005)

Organ	Index	Description	Maturity^A assumption
Female			
Ovary	$O = 1$	Largest follicles white and of diameter <2 mm	Immature
	$O = 2$	Largest oocytes yolking and of diameter 2 to 3 mm	Immature
	$O = 3$	Largest oocytes with yellowish yolk and of diameter >3 mm	Mature
	$O = 4^B$	Yolked oocytes of diameter >3 mm and corpora atretica readily visible	Mature
Uterus	$U = 1$	Uniformly thin, tubular structure	
	$U = 2$	Thin, tubular structure, partly enlarged posteriorly	
	$U = 3$	Uniformly enlarged, tubular structure	
	$U = 4$	*In utero* eggs present without macroscopically visible embryos present	
	$U = 5$	*In utero* embryos macroscopically visible	
	$U = 6$	Enlarged, tubular structure distended	
Male			
Seminal vesicle	$V = 1$	Thin, translucent walls and seminal fluids absent	Immature
	$V = 2$	Thickened, opaque walls and seminal fluids present	Mature
	$V = 3$	Thickened, opaque walls and seminal fluids absent	Mature
Testis	$t = 1$	Thin tissue strip with epigonal gland predominant	Immature
	$t = 2$	Thickened strip with epigonal gland tissue extensive	Immature
	$t = 3$	Enlarged and predominant with epigonal gland tissue negligible	Mature
Clasper^B	$C = 1$	Pliable with no calcification	Immature
	$C = 2$	Partly calcified	Immature
	$C = 3$	Rigid and fully calcified	Mature
Spermatogenesis	$S = 1$	Microscopically visible spermatocytes at Stage <17 (Mellinger 1965)	Immature
	$S = 2$	Microscopically visible spermatocytes at Stages 17 to 18 (Mellinger 1965)	Mature

^{A}Uterus condition was adopted for classing maternal condition; ^{B}Adopted for periods 1986–87 and 1998–01, but not for period 1973–76.

(ANCOVA) (with the terms SBC, covariate TL and SBC × TL interaction) was adopted to test for the effects of factor SBC on the body mass-TL relationship, where $\ln(a)$ and b are linear functions of SBC. ANCOVA was undertaken using the generalised linear modelling procedure ('Proc GLM') of the computer statistical package SAS (version 8.02) (SAS Institute, Cary, North Carolina, USA). Where the ANCOVA indicated statistically significant effects, the slopes and elevations of the linear relationships $\ln(w) = \ln(a) + b\ \ln(l)$ were statistically compared using the least-squares means tests in SAS. The various estimates of the parameters a and b and the statistical quantities required were obtained using the SAS regression procedure ('Proc Reg').

Litter size

The relationship between the number of macroscopically visible embryos *in utero*, p, and maternal TL, l, was determined using the exponential function $p = ce^{a'+b'l}$, where a' and b' are parameters estimated by linear regression $\ln(p) = a' + b'l$, and c is a coefficient for correcting bias caused by logarithmic transformation of p for the regression (Beauchamp and Olson 1973). ANCOVA (with the terms region, period, covariate TL, and interactions region × period, region × TL, period × TL and region × period × TL) was adopted to test for the effects of factors region and period, on the litter size-TL relationship, where parameters a' and b' are linear functions of region, period and region × period interaction. Starting with the interaction terms with the highest number of factors and covariate, the various terms were tested to sequentially exclude the terms with the highest statistically non-significant P-values ($P > 0.05$) until only significant terms remained. Once all non-significant interaction terms were eliminated, individual non-significant factors were eliminated (step-wise backward elimination). ANCOVA was undertaken using 'Proc GLM'. Where the ANCOVA had statistically significant effects, the slopes and elevations of the linear relationships $\ln(p) = a' + b'l$ were statistically compared using the least-squares means test in SAS. The various estimates of the parameters a' and b' and the statistical quantities required were obtained using 'Proc Reg'. Values of the constant c, required for the adjustment for biases caused by logarithmic transformation (Beauchamp and Olson 1973), were calculated separately.

Sex ratio of embryos and distribution of embryos and eggs between uteri

Paired t-tests were applied to the uterine contents of $U = 4$ and $U = 5$ pregnant females to test three null hypotheses. (1) The sex ratio of embryos is 1:1. (2) The number of embryos and infertile eggs in the left uterus equals the number in the right uterus for $U = 5$ females. (3) The number of eggs in the left uterus equals the number in the right uterus for $U = 4$ females. The SAS means procedure ('Proc Means') provided the differences in the means, the standard errors of the difference in the means, the values of the Student t-statistic, and probabilities of the differences in the means (Cody and Smith 1997). These tests were undertaken for each of the two regions WKI and EKI separately and for the two regions combined.

Period of gestation and embryonic growth

The growth pattern of embryos was determined from plots of mean TL of embryos (±s.d.) against month for each of the two regions WKI and EKI; mean TL values of 0 mm were assigned to eggs *in utero* for U = 4 females, but eggs *in utero* for U = 5 females were excluded. Patterns of wet mass gain or loss from egg to full-term embryo were investigated by separately plotting each of three variables against mean embryo TL from each U = 5 female. The variables were the (1) mean wet mass of embryos, (2) mean wet mass of external yolks and (3) mean wet mass of the external yolks expressed as a proportion of the sum of the mean wet mass of embryos and the mean wet mass of external yolks. Mean egg mass (±s.d.) for U = 4 females was plotted with mean wet mass of external yolks for a mean TL value of 0 mm.

Period of ovarian cycle

Preliminary examination of the data suggested that *M. antarcticus* had a biennial ovarian cycle in EKI and an annual ovarian cycle in WKI (present study) and in Western Australia (Lenanton *et al.* 1990). Determination of the period of the ovarian cycle in the mature females of a population is more complex where the ovarian cycle is ~2, 3, or more years than where it is ~1 year. Hence, the approach adopted to investigate the triennial ovarian cycle of *G. galeus* (Walker 2005) was followed in the present study. This involved examining seasonal growth patterns of the largest ovarian follicles in female *M. antarcticus* from the two regions WKI and EKI separately for each of the six uterus conditions (Table 1).

Pregnant females with embryos (U = 5) provide the least ambiguous basis for determining seasonal growth rates of the largest follicles and for distinguishing between annual, biennial and longer ovarian cycles. Small embryos were observed during late January and large embryos were observed during late December. This provided an unambiguous period, close to one full year, that could be adopted for estimating annual rate of growth of the largest follicle diameter (LFD). The seasonal trend in LFD for U = 5 females could then be compared with the seasonal patterns in LFD for females in each of three other uterus conditions. Data on LFD from U = 3, U = 4 and U = 6 females mostly provided less definitive information on follicle growth and required careful interpretation.

Annual growth rate of the largest follicles for U = 5 females was determined by the relationship between LFD, o, and day of year t, using the linear function $o = a'' + b''t$, where a'' and b'' are parameters estimated by linear regression. ANCOVA (with the terms region, covariate day and region × day interaction) was adopted to test for the effects of factor region (WKI and EKI) on the LFD-day relationship, where a'' and b'' are a linear functions of region. Starting with the interaction term, the various terms were tested to sequentially exclude the terms with the highest statistically non-significant P-values ($P > 0.05$), until only significant terms remained (step-wise backward elimination). ANCOVA was undertaken using ‘Proc GLM’. Where the ANCOVA had statistically significant effects, the slopes and elevations of the LFD-day linear relationships were statistically compared using the least-squares means test in SAS. The various estimates of the parameters a'' and b'' and the statistical quantities required were obtained using ‘Proc Reg’. For each region, the regression line for U = 5 females was compared with the scattergrams of LFD against day of year for each of the U = 3, U = 4, and U = 6 females separately. U = 1 and U = 2 females were excluded from the analysis because of negligible follicle growth and a lack of seasonal trend.

Length-at-maturity and length-at-maternity

Maturity and maternity were each expressed as a function of TL by logistic equations (ogives) determined by probit analysis and tested for the effects of region and period by logistic regression. The proportion of the population of females and the proportion of males mature at any TL was determined by classing each shark in ‘mature condition’ or ‘immature condition’. For determining the parameters of logistic equations, mature sharks were assigned a maturity condition value of 1, whereas immature sharks were assigned a maturity condition value of 0. Similarly, the proportion of the population of females maternal at any TL was determined by classing each female in ‘maternal condition’ or ‘non-maternal condition’ and assigning a value of 1 or 0 respectively (Walker 2005).

A female was classed as in ‘mature condition’ if the largest ovarian follicle was >3 mm in diameter (approximate size when vitellogenesis begins following folliculogenesis); otherwise, it was classed as in ‘immature condition’. Most studies define the mature condition by the presence of enlarged follicles. This makes the concept of maturity subjective because the period of enlargement of follicles from folliculogenesis to ovulation can be a period of several years in some species. The definition of maturity adopted for the present study infers the ‘onset of maturity’, where the ovary is functional in terms of synthesis and secretion of hormones and growth of oocytes. However, the ovary has not necessarily been subjected to ovulation or the formation of corpora lutea or corpora atretica. Similarly, other reproductive organs may not yet be fully developed (Walker 2005).

Given the uncertainty of the best indicator of maturity of males, the results from four different methods (seminal vesicle condition, testis development, clasper calcification and spermatogenesis stage) adopted for distinguishing between the mature condition and the immature condition were compared (Table 1).

A female is defined as being in maternal condition at the time of capture if it would have contributed to recruitment during the next recruitment season, had it survived (Walker 2005). For *M. antarcticus*, a female is classed as in maternal condition if it would have given birth to young 2 to 3 months before the next 1 January or shortly thereafter. This date was selected because it approximates the end of the parturition period occurring predominantly during November–December. This is also because the gestation period is ~12 months and eggs *in utero* occur predominantly between October and January following ovulation. Hence, a female was classed as in maternal condition if it met any one of three criteria based on uterus condition. These criteria were pregnant with macroscopically visible embryos between January and December (U = 5), pregnant with *in utero* eggs during January (U = 4), or non-pregnant and post partum with distended uteri between November and December (U = 6). All other females were classed as being in non-maternal condition;

i.e. U = 1, 2, or 3 between January and December; U = 4 between February and December; U = 5 with full-term embryos after December; or U = 6 between January and October (see 'Results' and 'Discussion').

The relationship between the proportion of sharks mature or maternal, P_l, and TL or length class, l, was determined using the logistic function $P_l = c'''[1 + e^{-(a''' + b'''l)}]^{-1}$, where a''', b''', and c''' are parameters. Parameter c''', which can take a value in the range 0 to 1, was fixed (see below) and parameters a''' and b''', with 95% confidence intervals, were estimated by maximum likelihood using a modified Newton–Raphson algorithm. Parameter $c''' = 1 - P_{Max.(l)}$, where $P_{Max.(l)}$ is the maximum proportion of sharks in mature condition or maternal condition. The standard error for any value of l is given by $\text{s.e.}_l = \sqrt{P_l}(1 - P_l) \times N^{-1}$. 'Proc Logistic' (with terms region, period, TL, region × period, region × TL, period × TL and region × period × TL was adopted to test for the effects of factors region and period on the P_l-l relationship, where parameters a''' and b''' are linear functions of region, period and region × period interaction, $P_l = n_l/N_l$, $\ln(P_l/1 - P_l) = -(a''' + b'''l)$, n_l is number of sharks mature or maternal and N_l is the total number of sharks of TL or length class, l, sampled for maturity or maternity (Walker 2005).

Changing from the regions of SA and BS adopted for the sampling design to the regions of WKI and EKI for statistical analysis had the effect of markedly reducing sample sizes for WKI and increasing sample sizes for EKI. Hence, for most of the analyses, the model design of the two factors of region and period had to be amalgamated to provide the single factor of region-period. The two regions (WKI and EKI) × three periods (1973–76, 1986–87 and 1998–01) (i.e. six region-periods) were reduced to four region-periods (EKI 1973–76, EKI 1986–87, EKI 1998–01 and WKI 1986–87). The two region-periods WKI 1973–76 and WKI 1998–01 had to be dropped from the analysis because of insufficient data. 'Proc Logistic' (with terms region-period, TL, and region-period × TL) was applied to test for the effects of the factor region-period.

Application of the SAS logistic and probit procedures required an additional step for the maternity analyses where parturition frequency (equal to $P_{\text{Max.}(l)}$) is not 1 year (Walker 2005). For *M. antarcticus*, parturition in EKI is biennial because about half the large females give birth each year ($P_{\text{Max.}(l)} = 0.50$), whereas parturition in WKI is annual because most large females give birth each year ($P_{\text{Max.}(l)} = 1.00$) (see 'Results' and 'Discussion'). This was undertaken by classing the number of females in maternal condition, n_l, and the total number of observations N_l, into 100-mm length classes. For parturition frequency in EKI, when the ratio of the number in maternal condition ($n_l \times N_l^{-1}$) within a 100-mm length class exceeded $P_{\text{Max.}(l)}$ (i.e. >0.50), the term n_l was adjusted to n'_l so that the ratio equalled $P_{\text{Max.}(l)}$; otherwise, $n'_l = n_l$. For input into logistic regression and probit analysis, the n'_l values were divided by $P_{\text{Max.}(l)}$ to ensure the ratio for the largest sharks was 1.00. In addition, a weight statement was used for logistic regression and probit analysis to weight the values in each length or length class by the original number of observations at that length or length class.

The relationship between P_l and l was initially tested for the effects of region, period and various interaction terms (Series 1 hypothesis testing) and then tested for the effects of region-period and the region-period × TL interaction term (Series 2 hypothesis testing). In each case, the model was run repeatedly, and the least statistically non-significant factor or interaction term was deleted at each sequential run of the model by the step-wise backward elimination procedure until only significant terms remained in the model. Interaction terms were eliminated before the factors. Where it was shown that the effects of region-period were statistically significant, planned region-period pair-wise comparisons were undertaken. Each step of the process of stepwise backward elimination and the pair-wise comparisons were tested using the Wald χ^2 likelihood-ratio test.

The SAS probit procedure sets $c'' = 0.00$ (i.e. $P_{\text{Max.}(l)} = 1.00$) by default. This is appropriate for the maturity ogive where all large females are mature, and hence the proportion of large-sized mature females in the population is 1.00 (i.e. $1 - c''$). Similarly, this is appropriate for maternity where all or most of the large females are in maternal condition (as in WKI). Hence, the proportion of large females in the population giving birth annually is 1.00; i.e. parturition frequency is annual ($P_{\text{Max.}(l)} = 1.00$). However, this is not appropriate where parturition frequency is biennial. The logistic relationships (with 95% CI) produced by the SAS probit procedure must be divided by $P_{\text{Max.}(l)}$ to give the required parameters of the maternity ogive with 95% CI. The SAS outputs must then be multiplied by $P_{\text{Max.}(l)}$, which was 0.5 for EKI.

In order to provide parameters that are more interpretable biologically, using outputs from SAS probit analysis, the logistic equation was reformulated as: $P_l = P_{\text{Max.}(l)}\{1 + e^{-\ln(19)[(l - l_{50})(l_{95} - l_{50})]}\}^{-1}$, where l_{50} and l_{95} are the lengths at which 50% and 95%, respectively, of the maximum proportion of sharks are in mature condition or maternal condition $P_{\text{Max.}(l)}$ (Walker 2005). The shape of these ogives (with 95% CI) and the various parameters of statistically significant region-periods were graphed and tabulated for visual comparison.

Seasonal variation in male breeding condition

Seasonal variation in the breeding condition of mature males was examined by separately testing for the effect of month on each of four variables: proportion of spermatocysts at various stages of spermatogenesis, fullness of seminal vesicles, GSI and HSI. In preparation for statistical analysis, available data for these variables were variously transformed. For spermatogenesis staging of each mature male (S = 2), the number of spermatocysts at each of the 18 stages of development (Mellinger 1965) counted along the transect was summed within each of four categories of stages. These categories are referred to as spermatogonia (Stages 1 to 6), spermatocytes (Stages 7 to 10), spermatids (Stages 11 to 14), and spermatozoa (Stages 15 to 18). The number of spermatocysts in each of the four categories was then expressed as a proportion of the total number of spermatocysts. Because the proportion of spermatocysts in each category for each mature male ranged from 0 to 1, the arcsine transformation was applied to proportion Y as $\sin^{-1}(\sqrt{Y})$ (Quinn and Keough 2002). GSI and HSI were expressed as a percentage of body mass (%GSI and %HSI). This avoided very small numbers and ensured that the transformed data were of the order of 1. For seminal vesicle fullness with seminal fluids in mature males (V = 2 to 3), the fullness indices 0, 1, 2, 3 and 4 were converted to the decimal values of 0.10, 0.25, 0.50, 0.75 and 1.00, respectively, and the decimal values Y' were then transformed to $\sqrt{\sqrt{Y'}}$. The effects of month and, where sufficient data were available, region were tested by ANOVA using 'Proc GLM', and differences in the means of the transformed data were tested among months. Homogeneity of variance was tested by the Levene method (Cody and Smith 1997). For seminal vesicle fullness, and owing to a lack of homogeneity of variance (see 'Results'), the effect of month was tested by the Kruskal–Wallis method on Wilcoxon non-parametric rank-sums (using SAS procedure 'Proc Npar1way') (Cody and Smith 1997) for each region separately. By expanding the model to include TL as a covariate in an ANCOVA, the mostly minor effect of TL was tested, and was then adjusted by least-squares means. To illustrate seasonal variation in male breeding condition, unadjusted mean monthly values of the four response variables (proportion of spermatocysts producing spermatozoa, %HSI, %GSI and seminal vesicle fullness) and values of these variables adjusted for the effect of TL were presented together for each region.

Results

Total body mass and total length

The largest female shark captured (1852 mm TL) was much longer than the largest male captured (1482 mm). The highest total body mass recorded for a female (24.8 kg) was almost double the highest mass recorded for a male (13.5 kg).

The effects of SBC on the body mass-TL relationship were tested for 861 males, 764 non-pregnant females, 30 pregnant females with eggs *in utero*, and 112 pregnant females with embryos *in utero*. The effects on the relationship were highly significant for SBC (ANCOVA: $F_{3,1759} = 15.55$, $P < 0.0001$), the covariate $\ln(l)$ (ANCOVA: $F_{1,1759} = 2275.89$, $P < 0.0001$) and the SBC × $\ln(l)$ interaction (ANCOVA: $F_{3,1759} = 17.38$, $P < 0.001$). Least-squares means tests indicated that males were highly significantly different from non-pregnant females ($P < 0.001$), but were not significantly different from pregnant females with eggs ($P = 0.0883$) or pregnant females with embryos ($P = 0.1855$). Similarly, least-squares means tests indicated that non-pregnant females were not significantly different from pregnant females with eggs ($P = 0.7574$) or pregnant females with embryos ($P = 0.3225$). Pooling data for all pregnant females produced a similar pattern of results.

The effect of sex on the body mass-TL relationship was then tested for 861 males and 1077 females; this test included an additional 171 females of unknown breeding condition. The effects on the relationship were highly significant for sex (ANCOVA: $F_{1,1934} = 34.97$, $P < 0.0001$), the covariate $\ln(l)$ (ANCOVA: $F_{1,1934} = 27975.2$, $P < 0.0001$) and the SBC × $\ln(l)$ interaction (ANCOVA: $F_{1,1934} = 38.80$, $P < 0.0001$). A least-squares means test indicated that males were highly significantly different from females ($P < 0.0001$). Hence, the relationships of total body mass against TL, with 95% CI on the mean curves and 95% prediction intervals for the data, are presented separately for females (Fig. 2*a*) and males (Fig. 2*b*). These curves indicate that for a given length >700 mm, the mean body mass is higher for females than for males (Fig. 2*c*).

Litter size

The number of macroscopically visible embryos *in utero* ranged from 1 to 57 and maternal TL ranged from 842 to 1852 mm for 137 $U = 5$ pregnant females from regions WKI and EKI during the sampling periods 1973–76, 1986–87 and 1998–01. The largest sample sizes were taken from EKI during 1973–76 ($n = 53$) and from WKI during 1986–87 ($n = 47$). Sample sizes were much smaller for EKI during 1986–87 ($n = 15$) and 1998 to 2001 ($n = 12$) and for WKI during 1973–76 ($n = 6$) and 1998–01 ($n = 4$). Step-wise backward elimination of statistically non-significant terms in the ANCOVAs testing the effects of region, period and region × period on the litter size-TL relationship indicated that region (ANCOVA: $F_{1,134} = 6.79$, $P = 0.0102$), TL (ANCOVA: $F_{1,134} = 214.24$, $P < 0.0001$) and interaction term region × TL (ANCOVA: $F_{1,134} = 6.79$, $P = 0.0191$) were statistically significant. This indicates that the litter size-TL relationship for $U = 5$ females was significantly different between WKI and EKI. Because period and each interaction term with period was not statistically significant, data were pooled by region and the litter size-TL relationship was determined for each of WKI and EKI (Fig. 3).

Sex ratio of embryos and distribution of embryos and eggs between uteri

The overall mean number (±s.e.) of visible embryos and infertile eggs for 144 $U = 5$ pregnant females (57 from WKI and 87 from EKI) was 15.87 ± 0.80 (14.79 ± 0.80 embryos and 1.08 ± 0.16 infertile eggs). The mean number of embryos in the left uterus was not significantly different from the mean number of embryos in the right uterus. However, the number of infertile eggs in the left uterus (0.68 ± 0.12) was significantly different from the number of infertile eggs in the right uterus (0.40 ± 0.08) ($n = 144$, mean difference $= 0.28$, s.e. $= 0.11$, $t = 2.46$, $P = 0.0151$). The number of male embryos was not significantly different from the number of female embryos; 8% of the embryos were too small for their sex to be macroscopically identified. The number of eggs in the left uterus was not significantly different from the number of eggs in the right uterus for 14 $U = 4$ pregnant females (all from EKI).

Period of gestation and embryonic growth

Embryonic growth was determined from 54 $U = 5$ females and 1 $U = 4$ female in WKI and from 78 $U = 5$ females and 35 $U = 4$ females in EKI. The samples were treated separately for each region, but were pooled over the three sampling periods (Fig. 4). The presence of eggs for $U = 4$ females observed between October and January is evidence that ovulation in the population begins early October and continues for at least part of this 4-month period. This indicates that the first eggs ovulated and fertilised can remain *in utero* for up to 4 months before developing embryos become macroscopically visible. The presence of embryos between January and December indicates that the period of gestation was about one year. Whereas ovulation and embryonic growth might have differed by several weeks among individual pregnant females, there was generally strong synchrony within the population of pregnant females. Too few

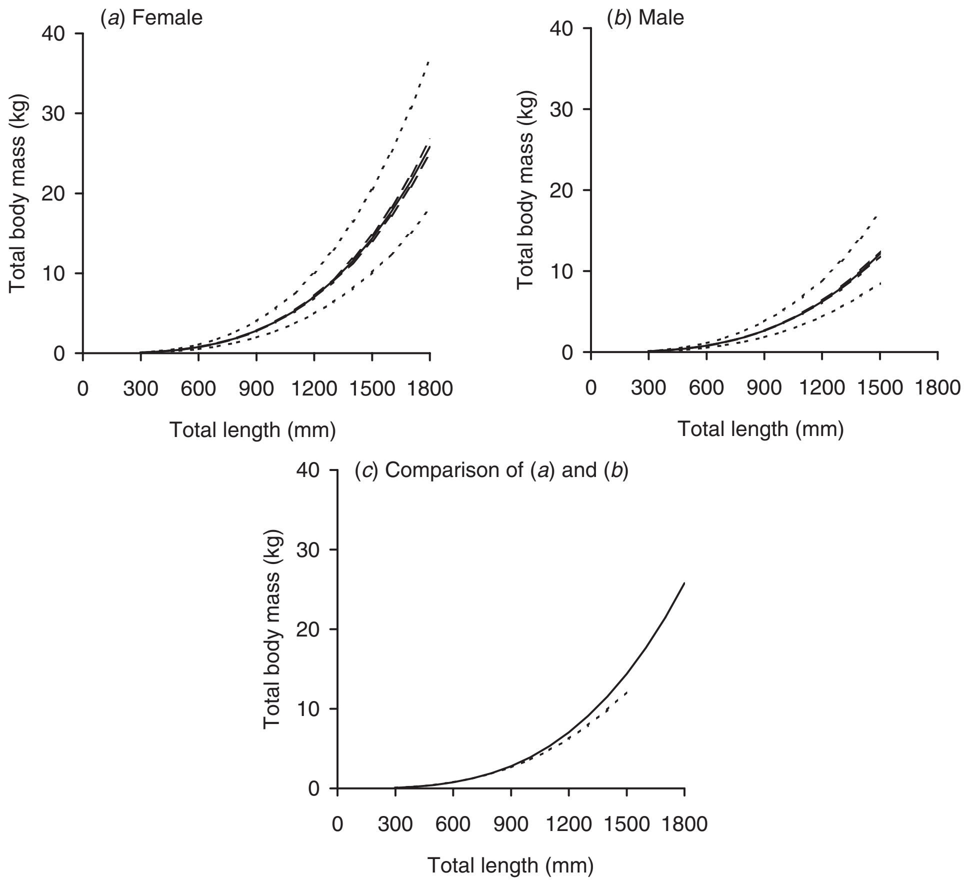

Fig. 2. Relationships between total body mass and total length of shark. Plots of mean total body mass against TL (——), with 95% confidence intervals (– – –) and 95% prediction intervals (- - - -), for (*a*) pregnant females, (*b*) non-pregnant females, (*c*) males and (*d*) comparison of the mean curves for pregnant females (——), non-pregnant females (– – –), and males (- - - -) in southern Australia during the periods 1973–76 and 1986–87 combined. Values of parameters and statistical quantities from linear regression analysis to derive the equation $w = acl^b$ are given in the following tabulation:

Shark category	a (s.e. range) $\times 10^{-9}$	b (s.e.)	c	n	r^2	rmse	P
Females	0.927 (0.790–1.089)	3.206 (0.023)	1.017	1077	0.947	0.185	***
Males	4.210 (3.450–5.120)	2.976 (0.029)	1.016	862	0.927	0.425	***

where w is total body mass, l is total length, a and b are parameters, c is the Beauchamp and Olson (1973) correction for bias from logarithmic transformation, n is sample size, r^2 is square of correlation coefficient, and rmse is root mean square error of for the regression equation $\ln(w) = a + b\ln(l)$. $*P < 0.1$; $**P < 0.01$; $***P < 0.001$.

pregnant females were collected from WKI between October and March to accurately determine the period of ovulation and to describe the early stages of gestation in this region. However, the similarity of the patterns of embryonic growth in pregnant females between WKI and EKI between April and September suggests that there was a high degree of synchrony across the two regions. These patterns indicate that parturition was complete by the end of December. However, anecdotal information from fishers suggests that a small proportion of large females in the population have full-term embryos as late as mid-January, at least during some years. The occurrence of two pregnant females in EKI during May that were carrying only eggs (i.e. designated U = 4) was interpreted as females being synchronously in phase with U = 5 females but bearing infertile eggs.

Full-term embryos reached a mean TL of ~330 mm during December (Fig. 4), a length indicative of TL at birth. For pooled WKI and EKI data, embryo wet mass increased curvilinearly with embryo TL; the highest mean mass of embryos from an individual pregnant female was 152 g for a 370-mm embryo mean TL (Fig. 5*a*). The mean wet mass of *in utero* eggs from 15 U = 4 females was 10.0 g (s.d. 2.6 g, range 3.7 to 21.9 g, $n = 253$ eggs) (Fig. 5*b*). Total body wet mass, external yolk wet mass and TL were recorded for 1766 embryos from 132 females. Among these U = 5 females, 54 also had 140 eggs (mostly infertile)

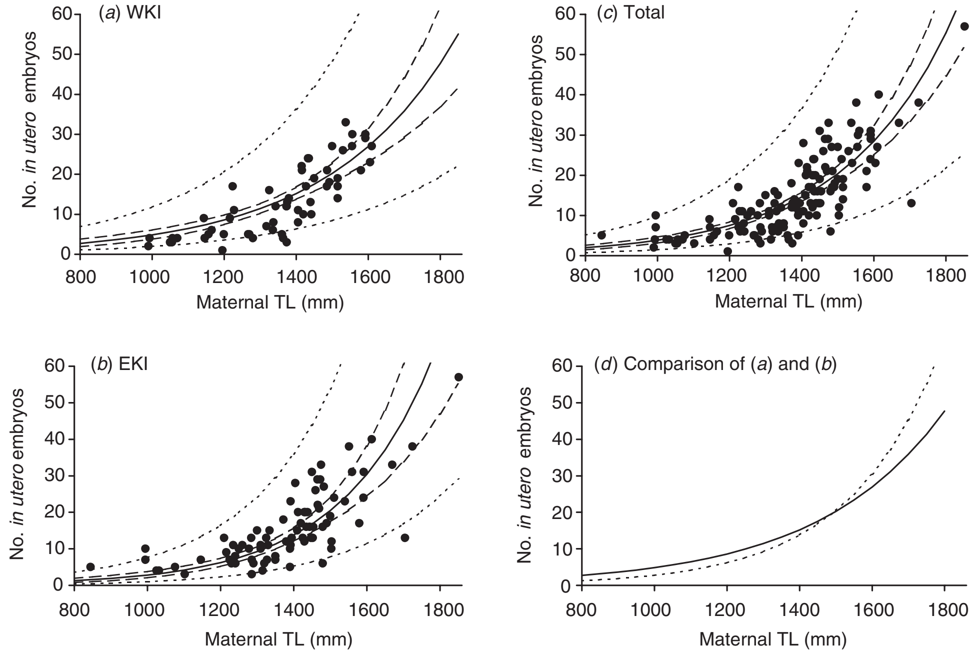

Fig. 3. Number of *in utero* embryos against maternal total length. Mean number of embryos (——), 95% confidence interval (– – –), 95% confidence intervals (- - - -) and raw points (●) are plotted against maternal TL of pregnant females from (*a*) west of Kangaroo Island (WKI), (*b*) east of Kangaroo Island (EKI), (*c*) these data combined and (*d*) comparison of the mean curves for WKI (——) and EKI (- - - - -). Values of parameters and statistical quantities for the equation $p = ce^{(a'+b'l)}$ are given in the following tabulation:

Region	a' (±s.e.)	b' (±s.e.)	c	n	r^2	rmse	P
WKI	−3.033 (±0.521)	0.00396 (±0.00038)	1.12	57	0.656	0.475	***
EKI	−1.376 (±0.394)	0.00286 (±0.00028)	1.10	80	0.560	0.433	**
Total	−2.087 (±0.324)	0.00333 (±0.00023)	1.11	137	0.595	0.463	***

where l is maternal TL measured in mm, p is number of embryos, a' and b' are parameters, c is Beauchamp and Olson's (1973) correction for bias from logarithmic transformation, n is sample size, r^2 is square of regression correlation coefficient after adjustment for multiple variables, rmse is root mean square error, and P is the probability of statistical significance for the linear regression $\ln(p) = a' + b'l$. $^*P < 0.1$; $^{**}P < 0.01$; $^{***}P < 0.001$.

in utero; 30 of these eggs could not be weighed because they were broken when handled. The mean wet mass of eggs from these 54 U = 5 females was 9.9 g (s.d. 5.0 g, range 2.5 to 23.0 g, $n = 110$ eggs), similar to the 10.0 g value obtained for the U = 4 females. The wet mass of external yolk sacs depleted rapidly during the first few months of gestation and the yolk reserves were mostly exhausted by mid-term, when embryo mean TL was ~200 mm and embryo mean mass was <25 g. There was a 10-fold mass gain from a mean wet mass of egg of 10 g to full-term embryo of ~100 g at 330 mm TL (Figs 5*a*–*c*). This indicates that there must be sources of nutrients additional to those provided by the yolk sac for embryonic growth.

Period of ovarian cycle

The LFD recorded in the ovary from each of 1000 females ranged from 1 to 28 mm. There was negligible difference in the diameters of the three largest follicles measured from 994 females (means were 4.8, 4.8 and 4.6 mm and s.e. was 0.2 mm for each); thus, for each female, only the first measured follicle, judged macroscopically as the largest, was used for statistical analysis. Trends in plots of LFD against day of year were not evident from all data pooled; seasonal patterns of LFD growth only became evident when the data were considered for each uterus condition (Figs 6 and 7). There was little variation in LFD among females in uterus conditions U = 1 (mean 1.6 mm, s.d. 0.9 mm, range 1 to 5 mm, $n = 183$) and U = 2 (mean 1.8 mm, s.d. 1.4 mm, range 1 to 11 mm, $n = 492$). Only 3% of the U = 2 females exhibited variation in LFD exceeding 1 to 5 mm, and this pattern was similar for WKI and EKI. LFD varied widely for U = 3 (range 1 to 28 mm, $n = 117$), U = 4 (range 4 to 25 mm, $n = 43$), U = 5 (range 2 to 23 mm, $n = 134$), and U = 6 (range 1 to 25 mm, $n = 31$). Patterns in LFD indicated that folliculogenesis or vitellogenesis had either not begun or were at an early stage for U = 1 to 2 females, but were more advanced for U = 3 to 6 females. As indicated earlier, the mass of eggs *in utero* varies widely (Fig. 5*b*), so it follows that LFD of ovulated oocytes (ova) also varies widely, but in general, follicles are ready for ovulation at ~20 mm diameter.

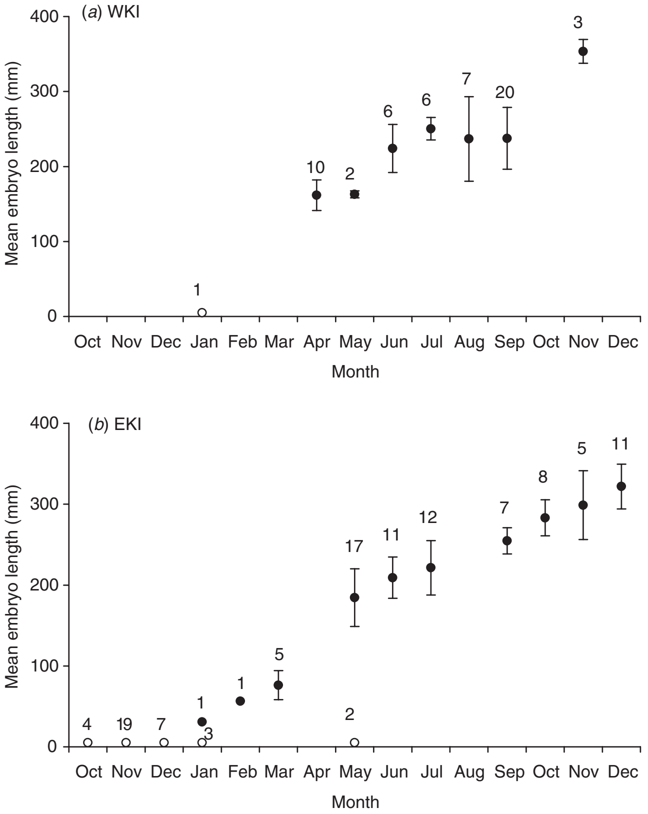

Fig. 4. Mean length of embryos against month. Mean monthly embryo length (*a*) from each of 54 U = 5 pregnant females with embryos and 1 U = 4 pregnant female with eggs only west of Kangaroo Island (WKI) and (*b*) from each of 78 U = 5 females and 35 U = 4 females east of Kangaroo Island (EKI); •, overall mean embryo length; bars, s.d.; ○, eggs; number above bar or symbol is monthly sample size.

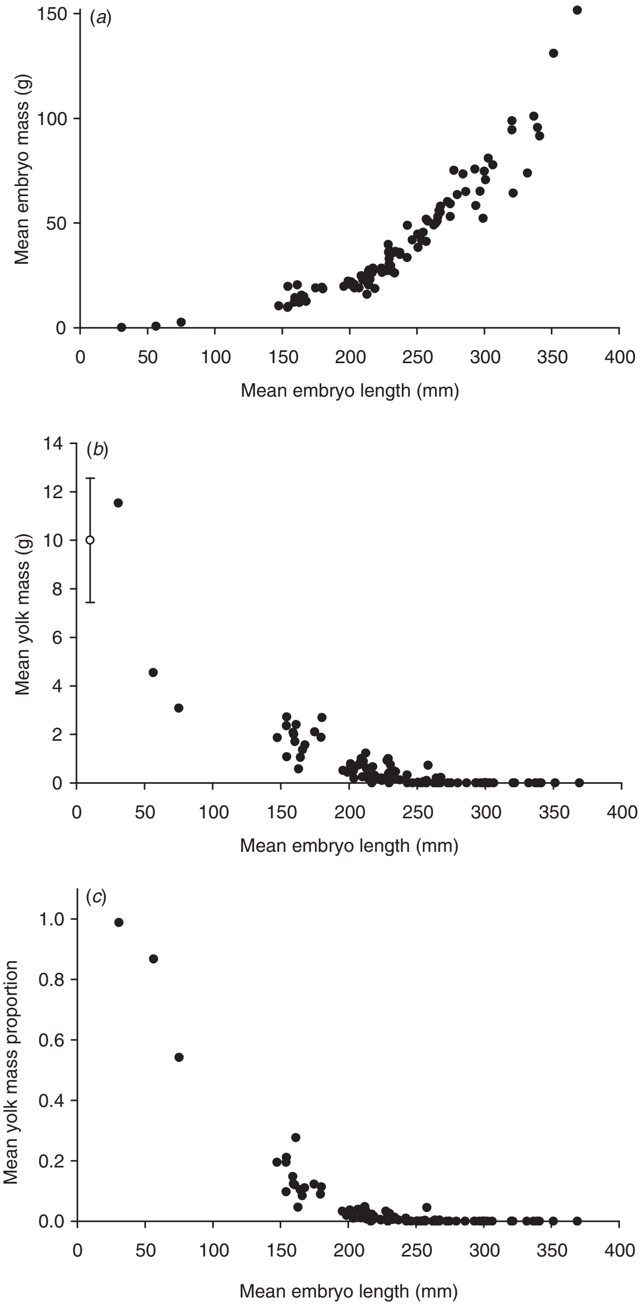

Fig. 5. Mean mass of embryos and yolk sacs against mean embryo length. (*a*) Mean mass of embryos, (*b*) mean mass of yolk sacs and (*c*) mean yolk sac mass as a proportion of sum of mean yolk sac and mean embryo mass {i.e. yolk sac mass × [embryo mass + yolk sac mass]$^{-1}$} against mean embryo length. Each data point represents mean embryo mass (•), mean yolk mass (•) or mean yolk mass proportion (•) and mean embryo length determined for the litter of each of 98 U = 5 pregnant females with embryos. Mean egg mass (○) shown in (*b*) was derived from 15 U = 4 pregnant females with eggs; bar, s.d. of egg mass.

Step-wise backward elimination of statistically non-significant terms in the ANCOVAs testing the effects of region and day of year (day) on the LFD-day relationship indicated that factor region (ANCOVA: $F_{1,130} = 3.19$, $P = 0.0766$) was close to being statistically significant, and both day (ANCOVA: $F_{1,130} = 123.15$, $P < 0.0001$) and interaction term region × day (ANCOVA: $F_{1,130} = 20.43$, $P < 0.0001$) were highly statistically significant. A least-squares means test indicated that the LFD-day relationship for U = 5 females was significantly different between WKI and EKI ($P < 0.0001$). The linear relationships indicate that mean annual growth of LFD in WKI (19.8 mm year^{-1}) (Fig. 7*a*) was about double that in EKI (8.4 mm year^{-1}) (Fig. 7*b* and Fig. 8). This indicates that, at the end of the year when gestation was complete or approaching completion, the ovarian follicles were large enough for ovulation in WKI but were only about half size in EKI. In WKI, the predicted mean LFD increased from −0.1 to 19.7 mm during one year, whereas in EKI the predicted mean LFD increased from 2.7 to 11.1 mm during one year. These different LFD growth rates are consistent with the hypothesis that the ovarian cycle is annual in WKI and biennial in EKI. Nevertheless, individual LFD values indicate that several females were exceptions to this hypothesis. In EKI, four females had LFD values that were well above the upper 95% prediction interval as they approached ovulation (Fig. 7*b*), suggesting that a small proportion of the females in EKI had an annual cycle.

Scattergrams of LFD against day of year for females in each of uterus conditions U = 3, U = 4 and U = 6 (Figs 7*c*–*h*) are

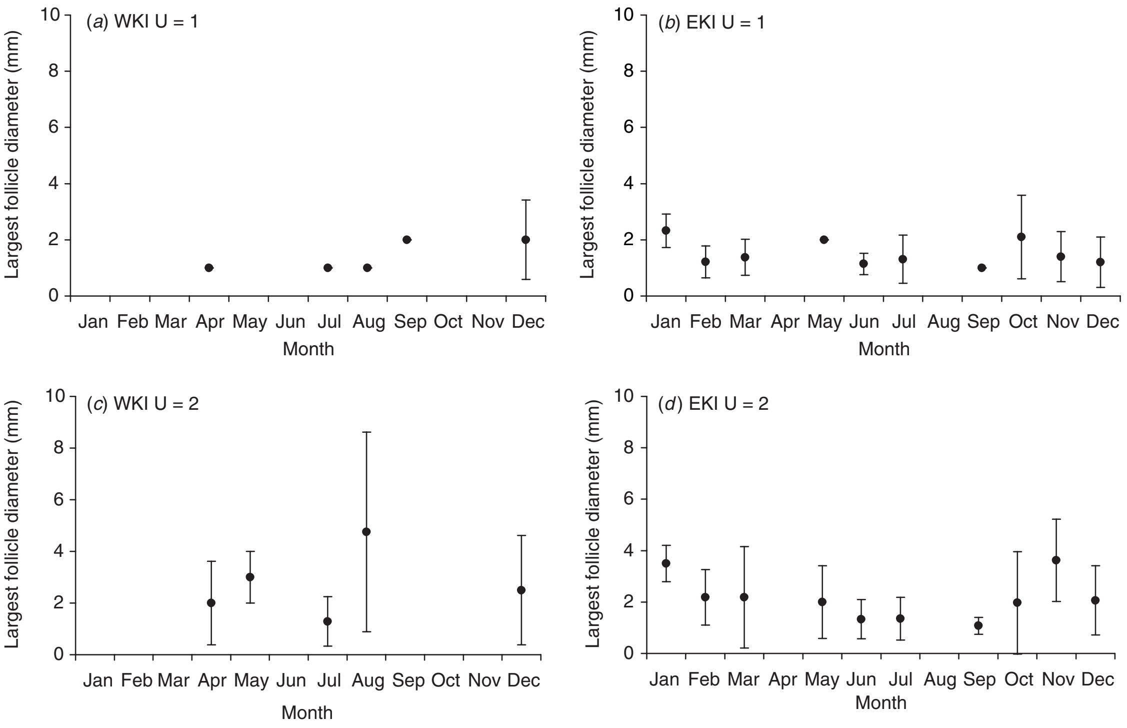

Fig. 6. Largest follicle diameter (LFD) against month by region for uterus conditions U = 1 and U = 2. Mean LFD (±s.d.) plotted against month for each of the two uterus conditions (*a* and *b*) U = 1 and (*c* and *d*) U = 2 from west of Kangaroo Island (WKI) (left) and east of Kangaroo Island (EKI) (right) during 1973–76, 1986–87 and 1998–01. Sample size (*n*) and annual mean LFD are given in the following tabulation:

Figure	U	Region	*n*	Mean mm (±s.d.)	Range (mm)
(*a*)	1	WKI	7	1.4 (0.8)	1–3
(*b*)	1	EKI	176	1.6 (0.9)	1–5
(*c*)	2	WKI	47	2.0 (1.8)	1–9
(*d*)	2	EKI	445	1.8 (1.3)	1–11

consistent with the hypothesis of a one-year cycle in WKI and a predominantly two-year cycle in EKI. In WKI, the data points clustered near the WKI U = 5 predicted mean LFD trajectory representing the one-year cycle, and clustered within its 95% prediction intervals plotted on each scattergram. Similarly, in EKI, the data points also clustered near the EKI U = 5 predicted mean LFD trajectory representing the two-year cycle, and clustered within its 95% prediction intervals. The EKI mean LFD trajectory is extrapolated through a second year and displayed graphically for a one-year period by presenting the trajectory as two parallel lines on each of the three EKI scattergrams. The bottom mean LFD trajectory and its lower 95% prediction interval represent the first year, and the top mean LFD trajectory and its upper 95% prediction interval represent the second year. The higher variation in LFD for any day of year in EKI than in WKI is consistent with the difference in the periods of the ovarian cycles.

The pattern of LFD against day of year for females with uterus condition U = 3 was similar to the pattern for females with U = 6 uterus condition in each of WKI and EKI. However, the pattern for females with U = 3 and U = 6 uterus conditions combined differed between WKI and EKI, while the patterns for females with U = 4 uterus condition were similar between WKI and EKI. The U = 6 uterus condition was expected to provide information on when parturition occurs, but these results are uncertain because it is difficult to macroscopically distinguish between the U = 3 and U = 6 uterus conditions. The pattern of LFD against day of year for the U = 4 uterus condition provides no information when attempting to distinguish between the hypothesis of a one-year ovarian cycle and that of a two-year ovarian cycle (Figs 7*e*, *f*). The data are consistent with either hypothesis, and therefore provide no support for one hypothesis over the other. However, these data for the U = 4 uterus condition do provide reliable information on the timing of ovulation and on the magnitude of LFD at the time of ovulation. The U = 4 females were classed as 'ovulating' or 'ovulated' on the basis of LFD, which has two size clusters ranging 4 to 11 and 15 to 25 mm LFD. U = 4 females were classed as ovulating (in the process of ovulation) if LFD ≥ 13 mm and were classed as ovulated (ovulation complete) if LFD < 13 mm. Ovulating females ($n = 11$) were captured from 6 October (Day 279) to 17 December (Day 351) in EKI, but only one ovulating female was captured (on 4 December, Day 338) in WKI. Ovulated females ($n = 31$) were captured during the period from 13 November (Day 317) to 18 December (Day 352) in EKI, but none were

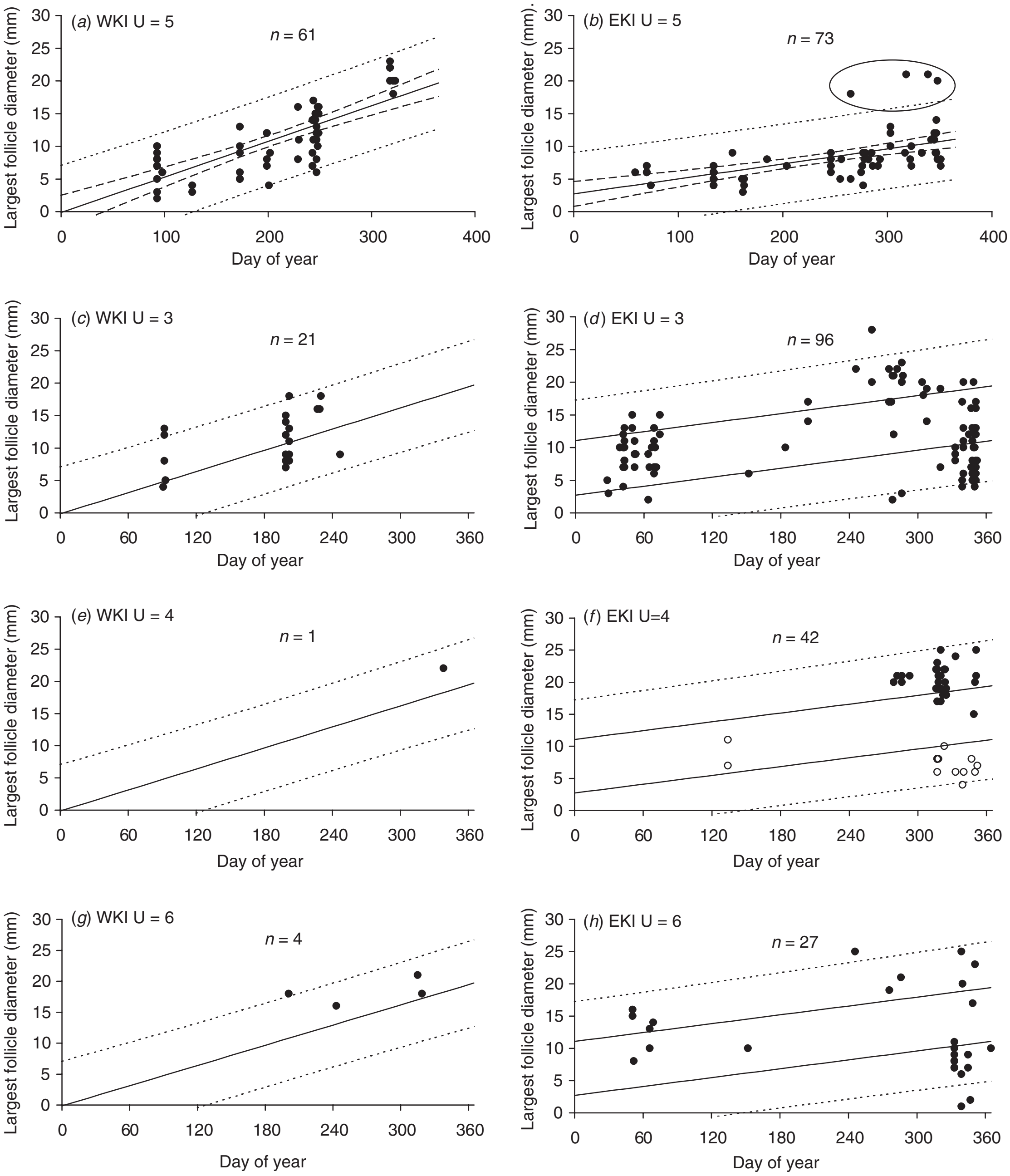

Fig. 7. Largest follicle diameter (LFD) against day of year by region for uterus conditions U = 3 to 6. LFD against day of year for females from west of Kangaroo Island (WKI) (left) and east of Kangaroo Island (EKI) (right) during 1973–76, 1986–87 and 1998–01 for each of four uterus conditions. Mean LFD (——) with 95% confidence intervals (– – – –) and 95% prediction intervals (- - - - -) are presented for (*a* and *b*) U = 5 pregnant females with embryos, (*c* and *d*) U = 3 non-pregnant females, (*e* and *f*) U = 4 pregnant females with eggs (ovulating, ●, and ovulated, ○) and (*g* and *h*) U = 6 post partum females. Values of parameters and statistical quantities for the regression equation $o = a'' + b''t$ for pregnant females with embryos are given in the following tabulation:

Uterus condition	Region	a'' (±s.e.)	b'' (±s.e.)	n	r^2	rmse	P
5	WKI	−0.142 (1.306)	0.0544 (0.0060)	61	0.575	3.362	***
5	EKI	2.712 (0.963)	0.0229 (0.0038)	73	0.324	3.023	***

where o is LFD, t is day of year, a'' and b'' are parameters, n is sample size, r^2 is square of regression correlation coefficient and rmse is root mean square error for the regression. Circled points in (*b*) are important outliers; they are exceptions to the biennial ovarian cycle in EKI. *$P < 0.1$; **$P < 0.01$; ***$P < 0.001$.

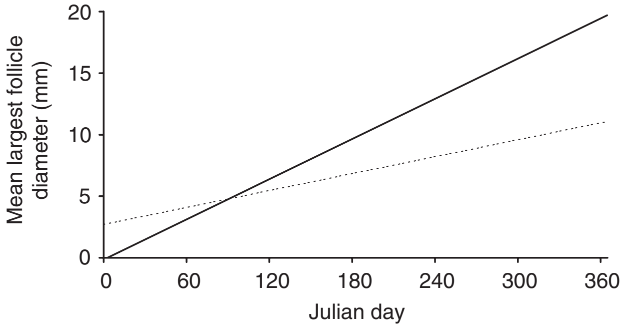

Fig. 8. Mean largest follicle diameter (LFD) against day of year by region for uterus condition $U = 5$. Mean LFD against day of year for $U = 5$ pregnant females with embryos from west of Kangaroo Island (WKI) (——) and east of Kangaroo Island (EKI) (- - - -) during 1973–76, 1986–87, and 1998–01 combined (from Fig. 7).

captured in WKI. Three females in uterus condition $U = 4$ were captured from 2 to 29 January, but could not be classed as ovulating or ovulated because LFD was not measured. In addition, two females with eggs *in utero* were captured in EKI on 14 May (Day 134); the LFD values of these females were 7 mm and 11 mm. One had 13 and the other 2 *in utero* eggs, and these eggs had crenate, slightly darkened surfaces and an appearance similar to that of the infertile eggs commonly found in $U = 5$ females. These two females, apparently in uterus condition $U = 4$, were interpreted as females ovulating ~6 months earlier in synchrony with females in uterus condition $U = 5$, but with infertile eggs *in utero*. These results indicate that ovulation occurred predominantly during November–December, with some individuals ovulating during October and January.

For a population with an annual ovarian cycle and a high degree of seasonal synchrony in LFD among individuals, it is feasible to pool LFD against day of year data across all uterus conditions where folliculogenesis or vitellogenesis has begun. This implies that data can be pooled for the $U = 3$, 4 (excluding ovulated females), 5 and 6 uterus conditions in WKI where there is an annual ovarian cycle. However, the data could not be pooled in EKI where there is a biennial ovarian cycle. For a two-year or longer cycle, it is not feasible to assign all the data points into the correct year of the ovarian cycle with a high degree of certainty. Hence, a linear regression fit to data of LFD against day of year in WKI for $U = 3$, 4 (where LFD $\geq$ 13 mm) and $U = 6$ females ($n = 26$) was compared with that for the $U = 5$ females ($n = 61$). This indicated that these two straight lines had neither significantly different slopes (t-test: $t = 0.242$, d.f. = 83 and $P > 0.025$) nor significantly different elevations (t-test: $t = 1.025$, d.f. = 83 and $P > 0.025$).

Both the stage of maturation as indicated by uterus condition and the stage of the ovarian cycle affected the mass of the ovary. Ovary mass was available only for females collected between 1973 and 1976, 135 females ($U = 1$ to 6) from EKI and 6 females ($U = 5$) from WKI. There was little change in ovary mass between $U = 1$ females (mean 3.9 g, s.d. 4.1 g, range 1 to 22 g, $n = 59$) and $U = 2$ females (mean 9.2 g, s.d. 7.7 g, range 1 to 22 g, $n = 14$). One large $U = 3$ female (1729 mm TL) had an exceptionally high value of 282 g ovary mass. The ovary mass for the other $U = 3$ females (mean 43.8 g, s.d. 28.8 g, range 10 to 98 g, $n = 17$) and $U = 4$ females (mean 32.3 g, s.d. 23.6 g, range 4 to 94 g, $n = 13$) was more variable. With the exception of one individual, the range of $U = 5$ females (mean 19.6 g, s.d. 17.8 g, range 4 to 69 g, $n = 36$) was narrower than that of $U = 3$ and $U = 4$ females. The exceptional $U = 5$ female, which was one of only two females observed in EKI carrying full-term embryos and close to ovulation, had a 195 g ovary mass. As might be expected from the LFD values, the few $U = 5$ females from WKI (mean 38.6 g, s.d. 8.3 g, range 25 to 47 g, $n = 6$) tended to have higher ovary mass than the $U = 5$ females from EKI. Ovary mass was weighed for only one $U = 6$ female (18 g).

The %GSI of $U = 1$ females (mean 0.14, s.d. 0.13, range 0.02 to 0.55, $n = 58$) was similar to that of $U = 2$ females (mean 0.16, s.d. 0.13, range 0.02 to 0.37, $n = 14$). The %GSI of $U = 3$, 4, 5 and 6 females was higher, with no obvious seasonal trends observed with the exception of $U = 5$ females. The %GSI of $U = 3$ females (mean 0.34, s.d. 0.14, range 0.13 to 0.67, $n = 16$) and $U = 4$ females (mean 0.35, s.d. 0.22, range 0.12 to 0.91, $n = 14$) exceeded the %GSI of $U = 5$ females (mean 0.19, s.d. 0.21, range 0.02 to 0.47, $n = 31$). The exception was one of the two $U = 5$ females from EKI close to ovulation, which had a %GSI of 1.17. Only one measurement was taken for $U = 6$ females (0.20).

The %HSI was similar for $U = 1$ (mean 4.26, s.d. 1.29, range 1.95 to 8.63, $n = 102$), $U = 2$ (mean 4.85, s.d. 1.24, range 2.02 to 7.65, $n = 18$), $U = 3$ (mean 4.50, s.d. 1.75, range 2.44 to 9.10, $n = 17$), $U = 5$ (mean 4.03, s.d. 1.67, range 1.77 to 11.55, $n = 57$) and $U = 6$ females (mean 4.43, s.d. 1.78, range 2.68 to 7.28, $n = 6$) females. Only $U = 4$ females (mean 7.08, s.d. 2.16, range 2.17 to 10.91, $n = 21$) were different. A weak but significant correlation between HSI and LFD (Spearman 0.321, $P < 0.01$) for $U = 3$ to 6 females provides some evidence for an increase in liver mass with vitellogenesis. There was no significant correlation between HSI and LFD (Spearman −0.213, $P > 0.05$) for $U = 1$ and 2 females.

Female length-at-maturity and length-at-maternity

Series 1 hypothesis testing for TL-at-maturity by step-wise backward elimination of statistically non-significant terms from the logistic regression model using Wald χ^2. likelihood-ratio tests indicated statistically significant interactions between region and period, between region and TL, and between period and TL. Series 1 hypothesis testing for TL-at-maternity gave similar results, except that the region × period interaction term was not statistically significant. Because of these significant interactions, Series 2 hypothesis testing had to be undertaken considering the data in the four region-periods EKI 1973–76, EKI 1986–87, EKI 1998–01 and WKI 1986–87. For both maturity and maternity, the two region-periods WKI 1973–76 and WKI 1998–01 were dropped from the analyses because of inadequate sample size largely caused by redefining the regions for data analysis purposes. Series 2 hypothesis testing for each of maturity and maternity indicated that both the period-region term and the region-period × TL interaction term were highly significant. Of six possible pair-wise comparisons between the four region-periods included in the analysis, three were significant for maturity and five were significant for maternity. For maturity, the significant differences were between EKI 1973–76 and EKI 1986–87, between EKI 1986–87 and WKI 1986–87, and between WKI 1986–87 and EKI 1998–01. For maternity, the only non-significant comparison was between EKI 1973–76 and EKI 1986–87 (Tables 2 and 3). This pattern justifies the separate presentation of the maturity ogive and the maternity ogive for each of the four region-periods EKI 1973–76, EKI 1986–87, EKI 1998–01 and WKI 1986–87 (Fig. 9).

When region-periods were compared, the patterns of significance differed between maturity and maternity. The $P_{\mathrm{Max.}(l)}$ value of maturity for all three EKI region-periods and for maternity in WKI 1986–87 was 1.00, whereas the $P_{\mathrm{Max.}(l)}$ value of maternity in the three EKI region-periods was 0.50 (Table 3). For maternity, the slightly downward adjustment of n_l to n'_l in each of several 100-m length classes where $P_{\mathrm{Max.}(l)} = 0.50$ might have also contributed to this difference in pattern of significance. The total number of maternal sharks was altered from 39 to 37.5 for EKI 1973–76, from 23 to 20.5 for EKI 1986–87 and from 50 to 45 for EKI 1998–01. No adjustment was made for WKI 1986–87 because $P_{\mathrm{Max.}(l)} = 1.00$ (Table 2).

As expected, the maternity ogives are to the right of the maturity ogives and the relative positions of the various region-periods are mostly similar for maturity and maternity, with one notable exception. In EKI, the maternity ogives moved sharply to the right from 1973–76 to 1986–87 and then moved part-way back towards the 1973–76 ogive from 1986–87 to 1998–01. In EKI, the maturity ogives followed this pattern with the exception of the 1998–01 ogive, which is to the right of the 1986–87 ogive. During 1986–87, the ogives for WKI are between the EKI 1973–76 and EKI 1986–87 ogives (but closer to EKI 1973–76) for both maturity and maternity. In general, the ogives tend to be much steeper for 1986–87 and 1998–01 than for 1973–76 (Fig. 9).

Male length-at-maturity

Male TL-at-maturity data were obtained from the seminal vesicle condition method and the testis development method during 1973–76, 1986–87 and 1998–01 and from the clasper calcification method during 1986–87 and 1998–01. Data were obtained from the spermatogenesis staging method only for EKI 1973–76 (Table 4).

Series 1 hypothesis testing by step-wise backward elimination of statistically non-significant terms from the logistic regression model using Wald χ^2. likelihood-ratio tests gave similar patterns of results for the seminal vesicle condition, testis development and clasper calcification methods. Region, period, TL and period × TL interaction were highly statistically significant for each method. Because one of the interaction terms was significant, Series 2 hypothesis testing had to be undertaken on the data from four region-periods: EKI 1973–76, EKI 1986–87, EKI 1998–01 and WKI 1986–87. As with the females, the two region-periods WKI 1973–76 and WKI 1998–01 were dropped from the Series 2 regressions because of inadequate sample sizes. Series 2 hypothesis testing indicated that both the factor region-period and the interaction region-period × TL terms were highly significant. Of the six pair-wise comparisons of each method, four were statistically significant and, where data were available, the pairs of significant region-periods were identical for the three macroscopic methods. The statistically significant comparisons existed between EKI 1973–76 and EKI 1986–87, between EKI 1973–76 and WKI 1986–87, between EKI 1973–76 and EKI 1998–01 and between EKI 1986–87 and EKI 1998–01. Only the comparisons between EKI 1986–87 and WKI 1986–87 and between WKI 1986–87 and EKI 1998–01 were not significant (Table 5). These differences indicate the need to separately present the maturity ogives for each of the four region-periods EKI 1973–76, EKI 1986–87, EKI 1998–01 and WKI 1986–87. These ogives are presented so that results can be compared among the four methods (Fig. 10).

Three of the four methods adopted mostly gave similar results, with the exception of the clasper calcification method, which consistently gave higher l_{50} and l_{95} values (ogive shifted to right) than did the other methods. The two methods of seminal vesicle condition and testis development gave very similar results, except WKI 1986–87 where the testis development method gave higher l_{50} and l_{95} values than did the seminal vesicle condition method. The results from the spermatogenesis staging method were very similar to those from the seminal vesicle condition and testis development methods for EKI 1973–76.

The patterns of difference among the various region-periods were similar across the methods. As with the females, the ogives tended to be much steeper during 1986–87 and 1998–01 than during 1973–76. In EKI, the ogives moved sharply to the right from 1973–76 to 1986–87 and then moved part of the way back towards the 1973–76 ogive from 1986–87 to 1998–01. During 1986–87, the ogives for EKI and WKI were similar (Fig. 10).

Seasonal variation in male breeding condition

The effect of month on %HSI was tested for 96 mature males (T = 3) collected from EKI over nine months (sample size only exceeded $n = 3$ in five of these months) during 1973–76; the sample size from WKI was too small for statistical analysis. For EKI, the effect of month was not significant (ANOVA: $F_{8,86} = 1.14$, $P = 0.3425$, $r^2 = 0.0962$). The condition of homogeneity of variance in %HSI among months was satisfied (Levene test: $F_{5,84} = 1.26$, $P = 0.2784$). However, the model became highly significant (ANCOVA: $F_{16,77} = 2.86$, $P = 0.0011$, $r^2 = 0.3725$) when covariate TL and month × TL interaction were added to the generalised linear model. The effects of the factor month (ANCOVA: $F_{7,77} = 4.04$, $P = 0.0008$) and the interaction month × TL (ANCOVA: $F_{7,77} = 4.05$, $P = 0.0008$) were highly significant, but the effect of covariate TL (ANCOVA: $F_{1,77} = 2.63$, $P = 0.1089$) was not significant. A depiction of the adjusted mean %HSI corrected by least-squares means for the effects of TL among months, where monthly sample size exceeded three males, indicates a slight peak in %HSI during May, but fairly constant %HSI during other times of the year (Fig. 11*a*).

The effect of month on the proportion of spermatocysts in each of the four categories of spermatogenesis stage (spermatogonia, spermatocytes, spermatids and spermatozoa) was tested on 112 mature males (S = 2) collected from EKI over 8 separate months during 1973–76. No data were collected from EKI during 1986–87 or 1998–01 or from WKI. The effect of month was highly statistically significant for spermatogonia (ANOVA: $F_{7,104} = 3.37$, $P = 0.0028$, $r^2 = 0.1851$) and for spermatozoa (ANOVA: $F_{7,104} = 4.39$, $P = 0.0003$, $r^2 = 0.2279$), but the effect of month was not significant for

Table 2. Female length-at-maturity and length-at-maternity sample sizes

A female was classed as in mature condition if the largest follicle diameter (LFD) was >3 mm; otherwise, it was classed as in immature condition. A female was classed as in maternal condition if U = 4 (Jan–Feb), U = 5 (Jan–Dec), or U = 6 (Nov–Dec); otherwise, it was classed as in non-maternal condition. For probit analysis, several values were marginally adjusted (**bold**) to prevent the ratio of the number of females in maternal condition/total number of animals examined within each 100-mm length class from exceeding 0.5 in EKI. Samples sizes of 2 immature and 6 mature females from WKI during 1973–76 and of 1 immature and 11 mature females from WKI during 1998–01 were inadequate for determining maturity ogives. Similarly, samples sizes of 2 non-maternal and 6 maternal females from WKI during 1973–76 and of 1 non-maternal and 11 maternal females from WKI during 1998–01 were inadequate for determining maturity ogives

Region	Period	Length class (mm)	Number classed mature			Number classed for each uterus index						Number classed maternal			
			Observed			1	2	3	4	5	6	Observed			Adjusted
			No	Yes	Total							No	Yes	Total	Yes
EKI	1973–76	<700	28		28	27	1					28		28	
		700–799	29		29	29						29		29	
		800–899	44	1	45	43	1			1		44	1	45	1
		900–999	45	2	47	42	3		1	1		46	1	47	1
		1000–1099	27	13	40	26	7	1	2	2		36	2	38	2
		1100–1199	12	20	32	9	9	4	1	1	2	23	3	26	3
		1200–1299	1	26	27	1		6	2	9		9	9	18	9
		1300–1399		23	23			1	5	6	1	6	7	13	**6.5**
		1400–1499	1	14	15			2	3	9		5	9	14	**7**
		1500–1599	1	10	11	1		3	1	5		5	5	10	5
		1600–1699		2	2			1	1			2		2	**1**
		≥1700		4	4			2		2		2	2	4	2
		Total	188	115	303	178	21	20	16	36	3	235	39	274	37.5
EKI	1986–87	<700	15		15	10	5					15		15	
		700–799	65		65	30	37					67		67	
		800–899	133	3	136	24	115	2				141		141	
		900–999	114	2	116	12	104	1		1		117	1	118	1
		1000–1099	84	6	90	3	87	1	1	1		92	1	93	1
		1100–1199	49	17	66	1	50	12	1	1	1	64	2	66	2
		1200–1299	11	42	53		20	30	3			53		53	
		1300–1399		17	17		1	4	2	8	2	7	10	17	**8.5**
		1400–1499		9	9			1		4	4	4	5	9	**4.5**
		1500–1599		4	4					2	2	1	3	4	**2**
		1600–1699		3	3						3	2	1	3	**1.5**
		≥1700													
		Total	471	103	574	80	419	51	7	17	12	563	23	586	20.5
EKI	1998–01	<700													
		700–799	6		6	6						6		6	
		800–899	41		41	40	1					41		41	
		900–999	80	2	82	77	4	1				82		82	
		1000–1099	61	8	69	52	13	1	1			67		67	
		1100–1199	48	16	64	22	32	7	4			63	2	65	2
		1200–1299	15	14	29	1	14	10	4		1	29	1	30	1
		1300–1399	6	24	30	1	4	8	9	6	2	20	10	30	10
		1400–1499	1	29	30		2	3	6	15	4	11	19	30	**15**
		1500–1599		18	18				6	7	5	8	10	18	**9**
		1600–1699	1	13	14		1		1	3	9	7	7	14	7
		≥1700		4	4				1	1	2	3	1	4	1
		Total	259	128	387	199	71	30	32	32	23	337	50	387	45
WKI	1986–87	<700													
		700–799	1		1	1						1		1	
		800–899	7		7	2	5					7		7	
		900–999	5	2	7	2	3			2		5	2	7	2
		1000–1099	20	11	31	2	20	5		4	1	28	4	32	4
		1100–1199	12	9	21		12	3		6		15	6	21	6
		1200–1299	3	19	22		8	8	1	5		17	5	22	5
		1300–1399	1	19	20			6		13	1	7	13	20	13
		1400–1499	2	7	9					9			9	9	9
		1500–1599		8	8					8			8	8	8
		1600–1699		2	2					2			2	2	2
		≥1700													
		Total	51	77	128	7	48	22	1	49	2	80	49	129	49

Table 3. Female length-at-maturity and length-at-maternity hypothesis testing

Testing for the effects of region (WKI and EKI) and period (1973–76, 1986–87 and 1998–01) on logistic regression of the proportion of females in mature or maternal condition against TL. A female was classed as in mature condition if the largest ovarian follicle diameter (LFD) was >3 mm; otherwise, the female was classed as in immature condition. A female was classed as in maternal condition if U = 4 (Jan–Feb), U = 5 (Jan–Dec) or U = 6 (Nov–Dec); otherwise, it was classed as in non-maternal condition. Results of Model Step 1 are not shown because no terms were statistically significant. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

Series	Model step	Source of variation	Maturity			Maternity		
			d.f.	χ^2	*P*	d.f.	χ^2	*P*
1 *Region (WKI and EKI) × Period (1973–76, 1986–87 and 1998–01)*								
	2	Region	1	6.6669	0.0098**	1	2315.3515	<0.0001***
		Period	2	7.8635	0.0196*	2	394.6825	<0.0001***
		TL	1	141.2649	<0.0001***	1	1841.1461	<0.0001***
		Region × Period	2	9.6108	0.0082**	2	0.0001	0.9933
		Region × TL	1	6.5843	0.0103*	1	18.3542	<0.0001***
		Period × TL	2	8.1868	0.0167*	2	250.6699	<0.0001***
		Residual	943			49		
	3	Region				1	48.3622	<0.0001***
		Period				2	236.7793	<0.0001***
		TL				1	1870.593	<0.0001***
		Region × TL				1	17.2989	<0.0001***
		Period × TL				2	253.6907	<0.0001***
		Residual				51		
2 *Region-period (WKI 1986–87, EKI 1973–76, EKI 1986–87 and EKI 1998–01)*								
	1	Region-period	3	13.7165	0.0033**	3	375.6253	<0.0001***
		TL	1	261.9350	<0.0001***	1	3367.9457	<0.0001***
		Region-period × TL	3	13.2608	0.0041**	3	366.4867	<0.0001***
		Residual	926			41		
		Pair-wise comparisons between region-periods						
		EKI 1973–76 and EKI 1986–87	1	4.0204	0.0450*	1	2.636	0.1045
		EKI 1973–76 and WKI 1986–87	1	2.9582	0.0854	1	53.501	<0.0001***
		EKI 1973–76 and EKI 1998–01	1	0.0380	0.8454	1	6.027	0.0141*
		EKI 1986–87 and WKI 1986–87	1	12.7128	0.0004***	1	49.801	<0.0001***
		EKI 1986–87 and EKI 1998–01	1	7.3939	0.0065**	1	35.647	<0.0001***
		WKI 1986–87 and EKI 1998–01	1	3.4447	0.0635	1	233.178	<0.0001***

spermatocytes or for spermatids. Tests for departure from homogeneity of variance for transformed proportion of spermatocysts was not significant for spermatogonia (Levene test: $F_{7,104} = 1.01$, $P = 0.4279$), spermatocytes, spermatids or spermatozoa (Levene test: $F_{7,104} = 1.38$, $P = 0.2196$), which allowed least-squares means between pairs of months to be tested for spermatozoa and spermatogonia. Differences in the proportion of spermatozoa were highly statistically significant for several pairs of months, and thus indicated a general pattern whereby the proportion of spermatozoa was higher during the later months of the year (September to December) than during the earlier months (February to June). Differences in the proportion of spermatogonia were also highly significant for various pairs of months; however, this proportion was generally lower during the later months of the year (September to December) than during the earlier months (February to June). The effect of adding covariate TL and month × TL interaction to the model, where $\sin^{-1}(\sqrt{Y})$ is the dependent variable, was statistically significant, but the effect was small when comparing the adjusted mean the proportion of spermatozoa (corrected by least-squares means for the effects of TL among months) with the unadjusted mean proportion of spermatozoa (Fig. 11*b*).

The effects of region and month on %GSI were tested on 135 mature males (T = 3) (102 from EKI and 33 from WKI) collected during 1973–76 and 1986–87. The generalised linear model of non-orthogonal design, was highly significant (ANOVA: $F_{13,121} = 4.35$, $P < 0.0001$, $r^2 = 0.3187$). The highly significant interaction region × month ($F_{2,121} = 5.44$, $P = 0.0055$) and factor month ($F_{10,121} = 3.54$, $P = 0.0004$) indicated that the effect of month differs between EKI and WKI; the factor region ($F_{1,121} = 2.92$, $P = 0.0903$) was not significant. Considering the effect of month in each region separately, departure from homogeneity of variance for transformed GSI was not significant in EKI (Levene test: $F_{7,91} = 0.86$, $P = 0.5405$) or WKI (Levene test: $F_{2,28} = 0.09$, $P = 0.9098$). The generalised linear model testing the effects of factor month on %GSI was not significant for EKI (ANOVA: $F_{9,92} = 1.11$, $P = 0.3640$), but was highly significant for WKI (ANOVA: $F_{3,29} = 23.11$, $P < 0.0001$). In WKI, although GSI data were only obtained for four months, least-squares means tests indicated that August was significantly different from each of May ($P = 0.0231$) and July ($P < 0.0001$), and that September was significantly different from each of May ($P = 0.0134$) and July ($P < 0.0001$). July was not significantly different from May ($P = 0.0789$)

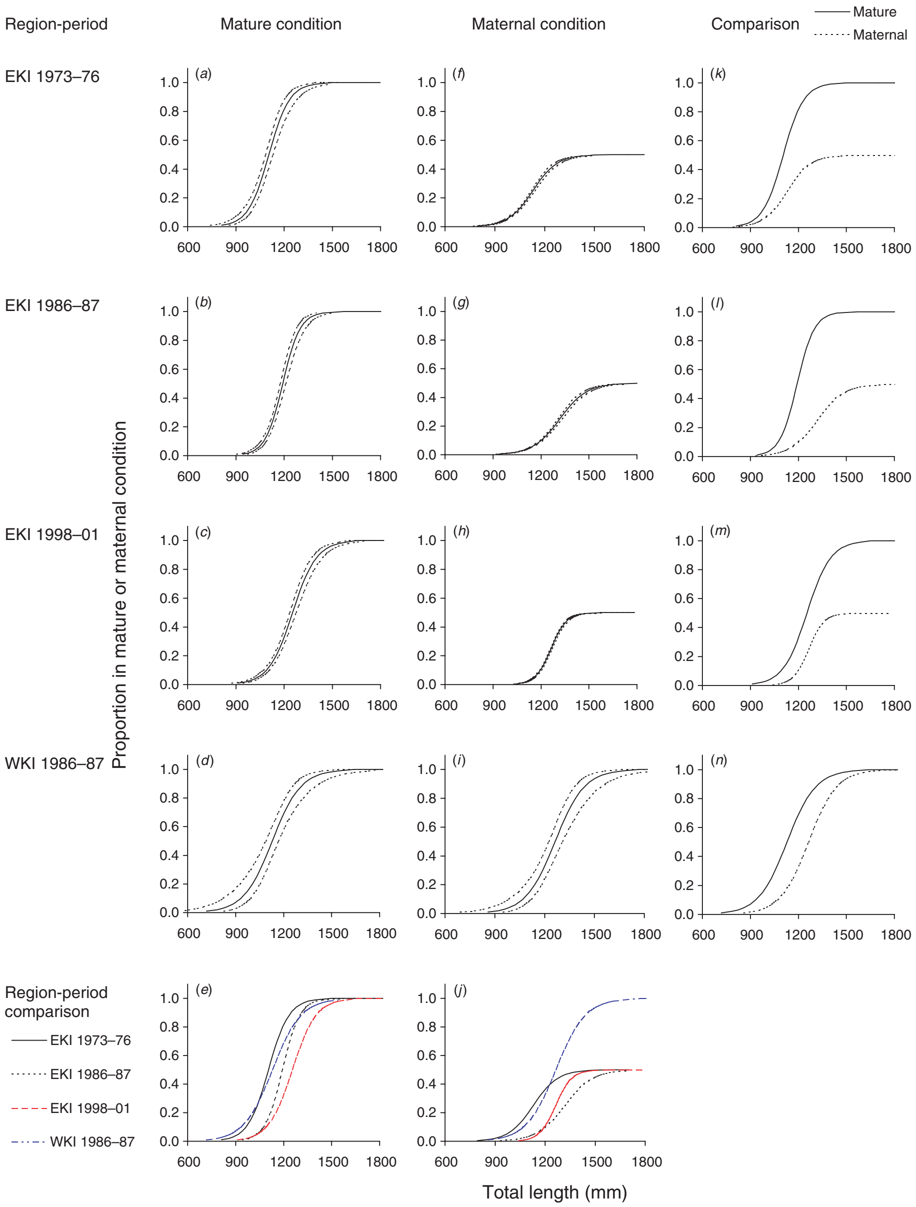

Fig. 9. Female length-at-maturity and length-at-maternity ogives for selected region-periods. Proportion of female population in mature or maternal condition against TL (——), with 95% confidence intervals (- - - - -), sampled from east of Kangaroo Island (EKI) during 1973–76, 1986–87 and 1998–01, from west of Kangaroo Island (WKI) during 1986–87, and various comparisons of these ogives. Values of parameters and statistical quantities for the equation $P_l = P_{\mathrm{Max}.(l)}\{1 + e^{-\ln(19)[(l-l_{50})(l_{95}-l_{50})]}\}^{-1}$ are tabulated in the following:

Figure	Condition	Region-period	l_{50} (CI)	l_{95} (CI)	$P_{\mathrm{Max}.(l)}$	n	N	ML	P
(*a*)	Mature	EKI 1973–76	1105 (1084, 1129)	1293 (1252, 1353)	1.00	115	303	−112.307	***
(*b*)		EKI 1986–87	1192 (1176, 1210)	1351 (1320, 1392)	1.00	103	574	−181.294	***
(*c*)		EKI 1998–01	1253 (1235, 1275)	1472 (1435, 1518)	1.00	128	387	−277.250	***
(*d*)		WKI 1986–87	1129 (1088, 1167)	1392 (1323, 1518)	1.00	77	128	−67.235	***
(*e*)		Comparison							
(*f*)	Maternal	EKI 1973–76	1129 (1118, 1140)	1344 (1322, 1370)	0.50	39 (37.5)	274	−1025.621	***
(*g*)		EKI 1986–87	1318 (1305, 1331)	1564 (1540, 1591)	0.50	23 (20.5)	586	−1991.618	***
(*h*)		EKI 1998–01	1263 (1257, 1296)	1405 (1394, 1417)	0.50	50 (45.0)	387	−1320.261	***
(*i*)		WKI 1986–87	1263 (1225, 1308)	1523 (1447, 1657)	1.00	49	129	−63.972	***
(*j*)		Comparison							
(*k*)		EKI 1973–76							
(*l*)		EKI 1986–87							
(*m*)		EKI 1998–01							
(*n*)		WKI 1986–87							

where l is TL measured in mm, P_l is proportion of females mature or maternal at TL l, l_{50} and l_{95} are parameters, $P_{\mathrm{Max}.(l)}$ is an asymptotic constant, n is the number of females classed in mature or maternal condition (adjusted in parentheses), N is the number of females examined for mature or maternal condition, ML is maximum likelihood and P is probability of statistical significance. $^{*}P < 0.1$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 4. Male length-at-maturity sample sizes for four separate methods

Number of males classed as mature or immature based on maturity indices for each length class and each of the four methods of seminal vesicle condition, testis development, spermatogenesis stage and, clasper calcification from EKI during 1973–76, 1986–87 and 1998–01, and from WKI during 1986–87. No data were collected from WKI during 1973–76 and insufficient data were collected from WKI during 1998–01 to include this region-period[A] in the analyses

Region-period	Length-class (mm)	Seminal vesicle condition						Testis development						Spermatogenesis or clasper calcification[B]					
		No. by index			No. classed mature			No. by index			No. classed mature			No. by index			No. classed mature		
		1	2	3	No	Yes	Total	1	2	3	No	Yes	Total	1	2	3	No	Yes	Total
EKI 1973–76	<600	18	0	0	18	0	18	19	0	0	19	0	19	2	0	–	2	0	2
	600–699	17	0	0	17	0	17	11	0	0	11	0	11	5	0	–	5	0	5
	700–799	35	5	0	35	5	40	25	2	5	27	5	32	13	1	–	13	1	14
	800–899	37	23	1	37	24	61	14	16	24	30	24	54	10	4	–	10	4	14
	900–999	48	19	6	48	25	73	12	28	21	40	21	61	10	19	–	10	19	29
	1000–1099	16	26	9	16	35	51	2	13	20	15	20	35	5	25	–	5	25	30
	1100–1199	4	32	21	4	53	57	1	2	32	3	32	35	3	33	–	3	33	36
	1200–1299	1	29	7	1	36	37	0	0	15	0	15	15	0	27	–	0	27	27
	1300–1399	0	8	1	0	9	9	0	0	2	0	2	2	0	5	–	0	5	5
	≥1400	0	1	0	0	1	1				0	0		0	1	–	0	1	1
	Total	176	143	45	176	188	364	84	61	119	145	119	264	48	115		48	115	163
EKI 1986–87	<600				0	0	0				0	0							
	600–699	10	0	0	10	0	10	10	0	0	10	0	10	6	0	0	6	0	6
	700–799	49	0	0	49	0	49	47	1	0	48	0	48	31	5	0	36	0	36
	800–899	86	4	0	86	4	90	86	2	2	88	2	90	70	18	5	88	5	93
	900–999	69	7	1	69	8	77	61	18	3	79	3	82	55	31	3	86	3	89
	1000–1099	26	22	5	26	27	53	21	17	20	38	20	58	14	33	10	47	10	57
	1100–1199	4	24	2	4	26	30	0	6	25	6	25	31	1	10	19	11	19	30
	1200–1299	0	12	0	0	12	12	0	0	13	0	13	13	0	4	12	4	12	16
	1300–1399	0	1	0	0	1	1	0	0	2	0	2	2	0	0	2	0	2	2
	≥1400	0	1	0	0	1	1	0	0	1	0	1	1	0	0	1	0	1	1
	Total	244	71	8	244	79	323	225	44	66	269	66	335	177	101	52	278	52	330
EKI 1998–01	<600																		
	600–699																		
	700–799	7	0	0	7	0	7	3	0	0	3	0	3	2	4	0	6	0	6
	800–899	63	6	0	63	6	69	24	0	3	24	3	27	25	69	0	94	0	94
	900–999	91	37	0	91	37	128	47	2	21	49	21	70	67	128	6	195	6	201
	1000–1099	25	58	4	25	62	87	15	3	27	18	27	45	33	78	39	111	39	150
	1100–1199	11	73	2	11	75	86	9	11	54	20	54	74	6	38	125	44	125	169
	1200–1299	0	64	1	0	65	65	1	0	50	1	50	51	2	10	120	12	120	132
	1300–1399	0	22	0	0	22	22	0	0	18	0	18	18	0	1	32	1	32	33
	≥1400	0	3	1	0	4	4	0	0	4	0	4	4	0	0	6	0	6	6
	Total	197	263	8	197	271	468	99	16	177	115	177	292	135	328	328	463	328	791
WKI 1986–87	<600																		
	600–699																		
	700–799																		
	800–899	5	1	0	5	1	6	5	0	1	5	1	6	5	0	1	5	1	6
	900–999	5	1	3	5	4	9	6	2	1	8	1	9	5	0	1	5	1	6
	1000–1099	6	17	4	6	21	27	4	8	13	12	13	25	7	10	9	17	9	26
	1100–1199	1	30	1	1	31	32	0	7	25	7	25	32	1	8	25	9	25	34
	1200–1299	0	21	1	0	22	22	0	1	21	1	21	22	0	2	20	2	20	22
	1300–1399	0	8	0	0	8	8	0	0	10		10	10	0	0	11	0	11	11
	≥1400	0	2	0	0	2	2	0	0	2		2	2	0	0	2	0	2	2
	Total	17	80	9	17	89	106	15	18	73	33	73	106	18	20	69	38	69	107

[A] 1 immature and 44 immature for seminal vesicle condition, 0 immature and 42 mature for testis development, 0 immature and 181 mature for clasper calcification collected from WKI during 1998–01, where all males were >1000 mm TL; [B] Samples for spermatogenesis were collected only from EKI during 1973–76; no samples for clasper calcification were collected from EKI during 1973–76.

and September was not significantly different from August ($P = 0.6728$). These results provide evidence for strong seasonality of GSI in WKI (higher during August–September than in May and July), but for weak or no seasonality of GSI in EKI. The effect of adding covariate TL and month × TL interaction to the ANCOVA was statistically significant, but the effect was negligible when comparing adjusted mean %GSI (corrected by least-squares means for the effects of TL among months) with

Table 5. Male length-at-maturity hypothesis testing for three separate methods

Testing for the effects of region (WKI and EKI), period (1973–76, 1986–87 and 1998–01), TL and their interactions by logistic regression of the proportion of males in mature condition against TL. These effects were tested separately for each of the three methods based on seminal vesicle condition, testis development and clasper calcification. Results of Model Steps 1, 2 and 3 are not shown because they contained terms that were not stastistically significant. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; nd, no data

Series	Model step	Source of variation	Seminal vesicle condition			Testis development			Clasper calcification		
			d.f.	χ^2	P	d.f.	χ^2	P	d.f.	χ^2	P
1		*Region (WKI and EKI) × Period (1973–76, 1986–87 and 1998–01)*									
	4	Region	1	19.7457	<0.0001***	1	11.8427	0.0006***	1	370.3134	<0.0001***
		Period	2	54.0795	<0.0001***	2	52.0549	<0.0001***	1	55.1711	<0.0001***
		TL	1	541.7139	<0.0001***	1	384.0637	<0.0001***	1	636.2748	<0.0001***
		Period × TL	2	43.9914	<0.0001***	2	38.3342	<0.0001***	1	63.4898	<0.0001***
		Residual	781			716			633		
2		*Region-period (WKI 1986–87, EKI 1973–76, EKI 1986–87 and EKI 1998–01)*[A]									
	1	Region-period	3	52.8966	<0.0001***	3	53.6286	<0.0001***	2	47.6940	<0.0001***
		TL	1	194.8618	<0.0001***	1	235.4310	<0.0001***	1	265.7786	<0.0001***
		Region-period × TL	3	43.8681	<0.0001***	3	41.7224	<0.0001***	2	45.0897	<0.0001***
		Residual	756			692			572		
		Pair-wise comparisons between region-periods									
		EKI 1973–76 and EKI 1986–87	1	32.8429	<0.0001***	1	46.2275	<0.0001***	–	–	–
		EKI 1973–76 and WKI 1986–87	1	5.5923	0.0180***	1	7.9336	0.0049***	–	–	–
		EKI 1973–76 and EKI 1998–01	1	26.9778	<0.0001***	1	38.5513	<0.0001***	–	–	–
		EKI 1986–87 and WKI 1986–87	1	0.0323	0.8574	1	2.2311	0.1353	1	0.0083	0.9274
		EKI 1986–87 and EKI 1998–01	1	6.2852	0.0122*	1	19.5758	<0.0001***	1	5.8356	0.0157*
		WKI 1986–87 and EKI 1998–01	1	1.1521	0.2831	1	0.6931	0.4051	1	2.0846	0.1488

[A] Region-period EKI 1973–76 is not included in the analysis for clasper calcification method because there were no data.

unadjusted mean spermatozoa proportion in EKI (Fig. 11*c*) and WKI (Fig. 11*d*).

The effect of month on seminal vesicle fullness in mature males was tested on 667 mature males (V = 2 to 3) (531 from EKI and 136 from WKI) collected during 1973–76, 1986–87 and 1986–87. Departure from homogeneity of variance for transformed data on seminal vesicle fullness was highly significant for EKI (Levene test: $F_{9,521} = 4.83$, $P < 0.0001$), but not for WKI (Levene test: $F_{5,129} = 1.33$, $P = 0.2563$), which prevented the use of ANOVA to test the effect of month in EKI. Non-parametric tests on Wilcoxon scores indicated that month was highly significant for each of EKI (Kruskal–Wallis test: $\chi^2_9 = 85.91$, $P < 0.0001$) and WKI (Kruskal–Wallis test: $\chi^2_6 = 71.43$, $P < 0.0001$). However, in EKI, there was no significant difference among months from October to March (Kruskal–Wallis test: $\chi^2_5 = 10.02$, $P = 0.0747$) or from May to September (Kruskal–Wallis test: $\chi^2_3 = 5.84$, $P = 0.1196$). In WKI, seminal vesicle fullness rose rapidly from September to November. There appears to be a seasonal pattern, and seminal vesicle fullness was higher in WKI than in EKI during most months. Appropriate adjustments for effects of TL by least-squares means did not affect the monthly pattern for EKI (Fig. 11*e*) or WKI (Fig. 11*f*).

Discussion

Total body mass and total length

The greater maximum TL of females compared with males as observed for *M. antarcticus* is common in mustelids, e.g. *M. canis* (Conrath and Musick 2002), *M. higmani* (Springer and Lowe 1963), *M. manazo* (Tanaka and Mizue 1979), *M. lenticulatus* (Francis and Mace 1980), *M. Mustelus* and *M. palumbres* (Smale and Compagno 1997), and consistent with most species of shark (Last and Stevens 1994). Several studies show that relationships of total body mass against TL differ such that females have a higher mass than males for a given length, e.g. *G. galeus* (Walker 2005), *Centroscyllium fabricii* and *Etmopterus princeps* (Jakobsdóttir 2001). As in *M. antarcticus*, the female and male curves for these relationships coincide for low values of TL, but diverge with increasing TL.

Litter size

Litter size varies widely among chondrichthyan species, but commonly increases with maternal TL. The curvilinear litter-size-maternal-TL relationship observed for *M. antarcticus* (Lenanton *et al.* 1990; present study) is also evident for other species, e.g. *M. lenticulatus* (Francis and Mace 1980) and *Rhizoprionodon terraenovae* (Loefer and Sedberry 2003). However, a linear relationship is more commonly found, e.g. *M. manazo* (Yamaguchi *et al.* 1997), *M. canis* (Conrath and Musick 2002), *M. mustelus*, *M. palumbres* (Smale and Compagno 1997), *G. galeus* (Walker 2005) and *Squalus acanthias* (Hanchet 1988). Spatial differences in the litter-size-maternal-TL relationship are evident for *M. antarcticus* between EKI and WKI (present study), and between EKI (present study) and Western Australia (Lenanton *et al.* 1990). Spatial differences also occur for *M. lenticulatus* in New Zealand waters (Francis and Mace 1980) and for *M. manazo* in Taiwanese and Japanese waters; the litter

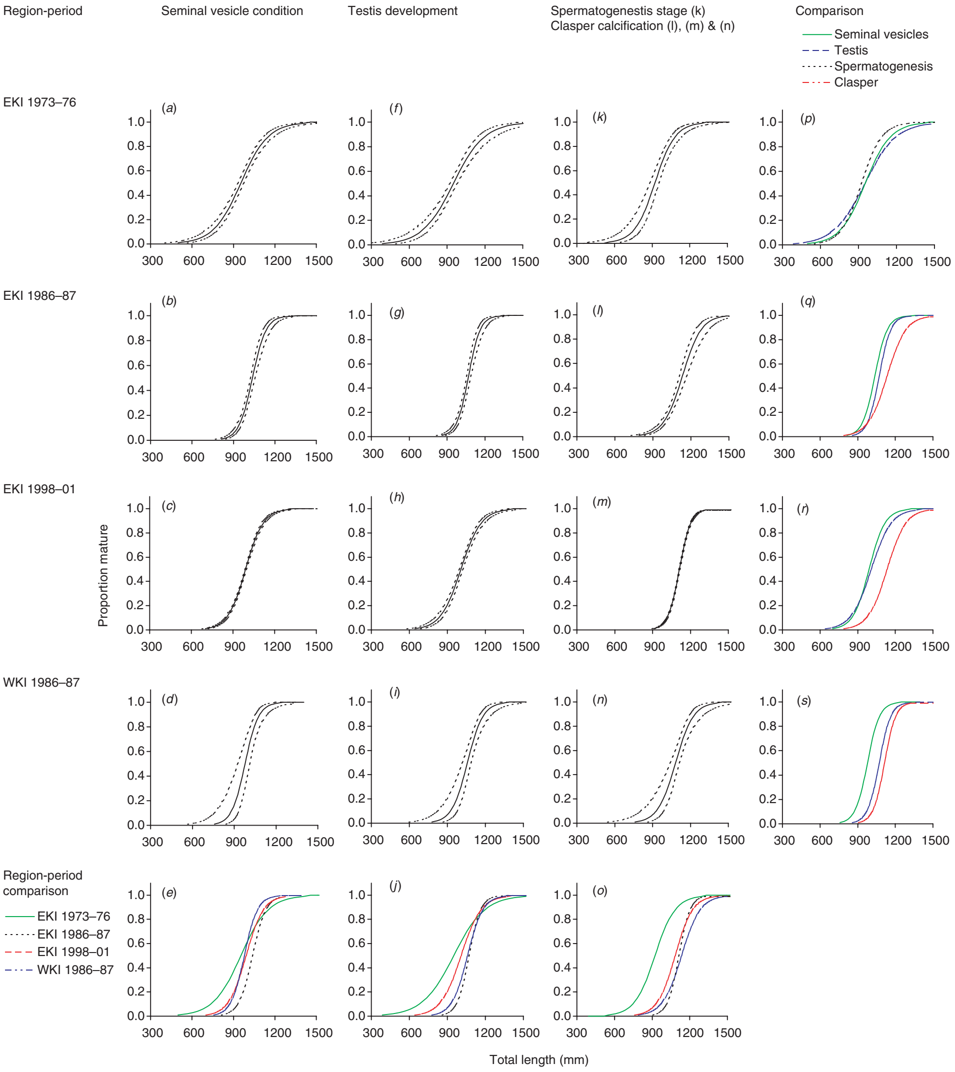

Fig. 10. Male length-at-maturity ogives for selected region-periods by four separate methods. Proportion of male population mature against TL (——), with 95% confidence intervals (- - - - -), sampled east of Kangaroo Island (EKI) during 1973–76, 1986–87 and 1998–01 and west of Kangaroo Island (WKI) during 1986–87 determined from the four methods of seminal vesicle condition, testis development, spermatogenesis stage and clasper calcification. Values of parameters and statistical quantities for the equation $P_l = P_{\mathrm{Max.}(l)}\{1 + e^{-\ln(19)[(l-l_{50})(l_{95}-l_{50})]}\}^{-1}$ are tabulated in the following:

Figure	Method	Region	Period	l_{50} (CI)	l_{95} (CI)	$P_{\mathrm{Max.}}$	n	N	ML	P
(*a*)	Seminal vesicle condition	EKI	1973–76	953 (932, 973)	1245 (1201, 1305)	1.000	188	364	−282.860	***
(*b*)	Seminal vesicle condition	EKI	1986–87	1037 (1022, 1055)	1181 (1151, 1224)	1.000	79	323	−140.494	***
(*c*)	Seminal vesicle condition	EKI	1998–01	991 (985, 997)	1177 (1162, 1195)	1.000	271	468	−1416.767	***
(*d*)	Seminal vesicle condition	WKI	1986–87	978 (925, 1010)	1119 (1082, 1192)	1.000	89	106	−30.597	***
(*e*)	Seminal vesicle condition	Comparison								
(*f*)	Testis development	EKI	1973–76	950 (922, 979)	1312 (1238, 1427)	1.000	119	264	−217.851	***
(*g*)	Testis development	EKI	1986–87	1070 (1055, 1089)	1206 (1176, 1249)	1.000	66	335	−124.646	***
(*h*)	Testis development	EKI	1998–01	1007 (993, 1021)	1241 (1212, 1279)	1.000	177	292	−399.011	***
(*i*)	Testis development	WKI	1986–87	1059 (1018, 1087)	1238 (1194, 1323)	1.000	73	106	−56.862	***
(*j*)	Testis development	Comparison								
(*k*)	Spermatiogenesis stage	EKI	1973–76	923 (882, 954)	1160 (1113, 1236)	1.000	115	163	−84.665	***
(*l*)	Clasper calcification	EKI	1986–87	1133 (1108, 1166)	1354 (1299, 1433)	1.000	52	330	−158.289	***
(*m*)	Clasper calcification	EKI	1998–01	1112 (1108, 1117)	1245 (1236, 1254)	1.000	328	791	−1542.165	***
(*n*)	Clasper calcification	WKI	1986–87	1083 (1040, 1112)	1289 (1237, 1395)	1.000	69	107	−65.991	***
(*o*)	Clasper calcification	Comparison								
(*p*)	Comparison	EKI	1973–76							
(*q*)	Comparison	EKI	1986–87							
(*r*)	Comparison	EKI	1998–01							
(*s*)	Comparison	WKI	1986–87							

where l is TL measured in mm, P_l is proportion of males mature at TL, l_{50} and l_{95} are parameters, $P_{\mathrm{Max.}}$ is an asymptotic constant, n is the total number of males mature, N is the total number of males examined for breeding condition, ML is maximum likelihood, and P is probability of statistical significance. $^{*}P < 0.1$; $^{**}P < 0.01$; $^{***}P < 0.001$.

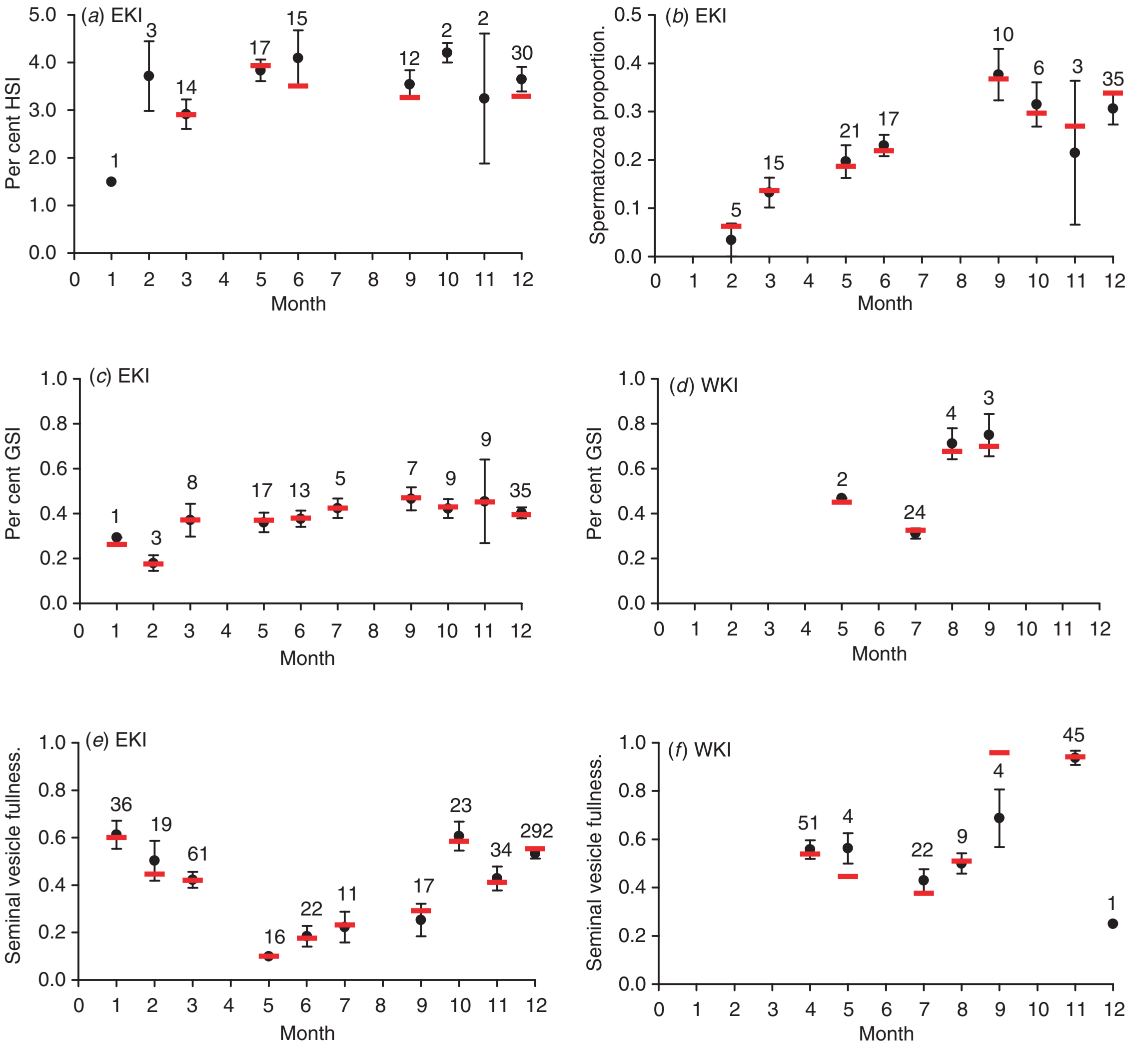

Fig. 11. Various breeding conditions against month for mature males. (*a*) Per cent hepatic somatic index (HSI) east of Kangaroo Island (EKI) during 1973–76, (*b*) mean proportion of spermatocysts at the stage of producing spermatozoa in EKI during 1973–76, per cent gonad somatic index (GSI) in (*c*) EKI and (*d*) west of Kangaroo Island (WKI) during 1973–76 and 1986–87, and seminal vesicle fullness in (*e*) EKI and (*f*) WKI during 1973–76, 1986–87 and 1998–01. ●, mean monthly value; bars, s.e. for monthly value; –, mean monthly value corrected for effect of TL of shark; number above bar is monthly sample size.

size of *M. manazo* at any maternal TL tends to fall from south to north, possibly with decreasing water temperature (Yamaguchi *et al.* 2000).

The lack of detectable temporal differences in the litter-size-maternal-TL relationship for *M. antarcticus* suggests a lack of density-dependent effects operating on litter size, given that large changes occurred in abundance between the sampling periods. A more extensive study investigating density-dependent effects for *S. acanthias*, taken by demersal trawl off the north-eastern coast of the USA from 1998 to 2002, indicates the lack of an annual difference in the litter-size-maternal-TL relationship (Sosebee 2005). However, an earlier study of this stock did detect a decrease in litter size with increasing stock abundance (Silva 1993). *Squalus acanthias* taken by demersal trawl off New Zealand exhibited subtle, but statistically significant annual differences in the litter-size-maternal-TL relationship between 1983 and 1985 (Hanchet 1988), at a time when large changes in abundance were unlikely.

Sex ratio of embryos and distribution of embryos and eggs among uteri

The sex ratio of 1:1 among embryos found for *M. antarcticus* (Lenanton *et al.* 1990; present study) is typical for shark species. This is the ratio found whenever large sample sizes are examined, and was previously recorded for e.g. *S. acanthias* (Hanchet 1988), *Squalus megalops* (Watson and Smale 1998; Braccini *et al.* 2006), and *G. galeus* (Walker 2005). The ratio of the number of embryos (or *in utero* eggs) in the left uterus to the number in the right uterus of pregnant females is rarely measured. The pattern of a 1:1 ratio of embryos and of *in utero* eggs between the uteri of *M. antarcticus* is similar to that of *G. galeus* (Walker 2005) and *Triakis semifasciata* (Ebert and

Ebert 2005). However, *G. galeus* has a 1:1 ratio of infertile eggs between the uteri in females pregnant with macroscopically visible embryos, whereas *M. antarcticus* was found to have a ratio of 0.68:0.40, which differed significantly from 1:1. This is not readily explainable. One suggestion proposed for other species is that the position of the stomach and other organs create asymmetric differences in the space available to the paired uteri in the coelomic cavity (Bass 1973; Braccini *et al.* 2006). Infertile or addled *in utero* eggs are not commonly reported but do occur in other species, e.g. *S. acanthias* (Hanchet 1988) and *G. galeus* (Walker 2005). In the present study, pregnant *M. antarcticus* were found to have a ratio of 14.8 embryos to 1.1 infertile eggs *in utero*; i.e. 93.2% embryos and 6.8% infertile eggs. However, there is potential for a slight overestimation of the proportion of infertile eggs because, during the early stages of gestation, some of the eggs classed as infertile might have subsequently developed as embryos. One pregnant female had seven embryos and five eggs; therefore, it follows that if some eggs are commonly unfertilised, then there will occasionally be females in which all *in utero* eggs are infertile. This is how the two females collected in May with only eggs *in utero* were interpreted.

Period of gestation, embryonic growth and period of pregnancy

The processes of ovulation and parturition within an individual female or within a population of a viviparous chondrichthyan species do not occur instantaneously, thus complicating definitions of ‘period of ovulation’, ‘period of parturition’, ‘period of gestation’ and ‘period of pregnancy’. Nevertheless, these terms require explicit definitions because they vary depending on whether the term applies to an individual female, a population or a species.

The period of gestation for an individual embryo is the period from its fertilisation to its birth. However, reported periods of gestation usually refer to a full litter, which is the period from fertilisation of the first ovum to birth of the last embryo as a neonate; this is better referred to as the period of pregnancy for a female. The period of pregnancy defined by the uterine conditions presented in Table 1 is the period from when the first fertilised egg appears *in utero* to the birth of the last full-term embryo. For an individual female, the definition of period of pregnancy necessarily includes the period of ovulation (period between release of first and last ovum) and the period of parturition (period between birth of first and last embryo). The period of pregnancy for a female has two components: the initial period in which the eggs are carried *in utero*, followed by the period in which macroscopically visible embryos are carried *in utero*. Parturition of a pregnant individual probably occurs over a short period, whereas ovulation is a more protracted process dependent on the number of ova serially released and lasting for up to several weeks or months. Inevitably, the period of pregnancy of an individual female is longer than the period of gestation of an individual embryo. Also inevitably, and owing to variation among individual females, the periods of pregnancy, ovulation and parturition are longer for a population than for an individual female. For a pregnant female with an annual reproductive cycle, the period of pregnancy must be 12 months or less, but for the entire population the period of pregnancy can be more than 12 months. For a species in which the females have a biennial, triennial or longer reproductive cycle, the periods of pregnancy and gestation can both exceed 12 months.

In EKI, *M. antarcticus* was observed at different stages of pregnancy during a 15-month period. Females were observed carrying eggs *in utero* during the 4-month period from October to January, and carrying embryos during the 12-month period from January to December (Fig. 12). In Western Australia, females were also observed at different stages of pregnancy during the ~15-month period from late November to early February (Lenanton *et al.* 1990). In this region, they were observed carrying eggs *in utero* during the ~3-month period from late November to early February, and carrying macroscopically visible embryos during the 13-month period from February to February (most were observed from February to December, but one female with full-term embryos was observed early February). These observations suggest that while there is a high degree of synchrony in the reproductive cycle among individual pregnant females in the population, some are out of phase with each other by up to 3 months. The observations also indicate that the peak modal timing of the individual cycles in Western Australia is 1 to 2 months behind that in EKI. There are insufficient data to precisely determine these periods for WKI, but they are expected to resemble those of Western Australia or to occur between those of Western Australia and EKI.

Within-population synchronous growth of embryos over a period of ~12 months is common for sharks, particularly among those inhabiting waters <300 m. Species in the Southern Hemisphere exhibiting an annual embryo growth pattern similar to that of *M. antarcticus* include *M. lenticulatus* (December to November) off New Zealand (Francis and Mace 1980), *M. mustelus* (December to November) off South Africa (Smale and Compagno 1997) and *G. galeus* (February to December, 11 months) in southern Australia (Walker 2005). Apart from being out of phase by 6 months, Northern Hemisphere species exhibiting this pattern include *M. canis* (July to May, 11 months) in the north-western Atlantic Ocean (Conrath and Musick 2002) and *M. manazo* (July to June, 10 to 12 months) in Japan (Yamaguchi *et al.* 2000). Similar to *M. antarcticus*, there are one- to two-month differences in the timing of the gestation period of *M. manazo* among five separate regions in Japan and Taiwan (Yamaguchi *et al.* 2000).

Squalids inhabiting relatively shallow coastal waters, such as *S. acanthias* and *S. megalops*, have periods of gestation that exceed 12 months, but *S. acanthias* populations exhibit synchronous gestation, whereas those of *S. megalops* are asynchronous. For example, gestation in *S. acanthias* off New Zealand occurs over 21 months from December to September, with each of two halves of the breeding population synchronising with the two halves that are out of phase by one year (Hanchet 1988). In contrast, gestation in *S. megalops* off southern Australia occurs over a similar period, but the timing among individuals is asynchronous (Braccini *et al.* 2006).

The 10-fold increase in wet-mass gain from egg to full-term embryo in *M. antarcticus* does not imply that there is a 10-fold increase in organic and inorganic material supplied by maternal nutrients during embryonic development. This is because of the high water content of both egg and embryo. Differences in the composition of eggs and full-term embryos of *Centrophorus*

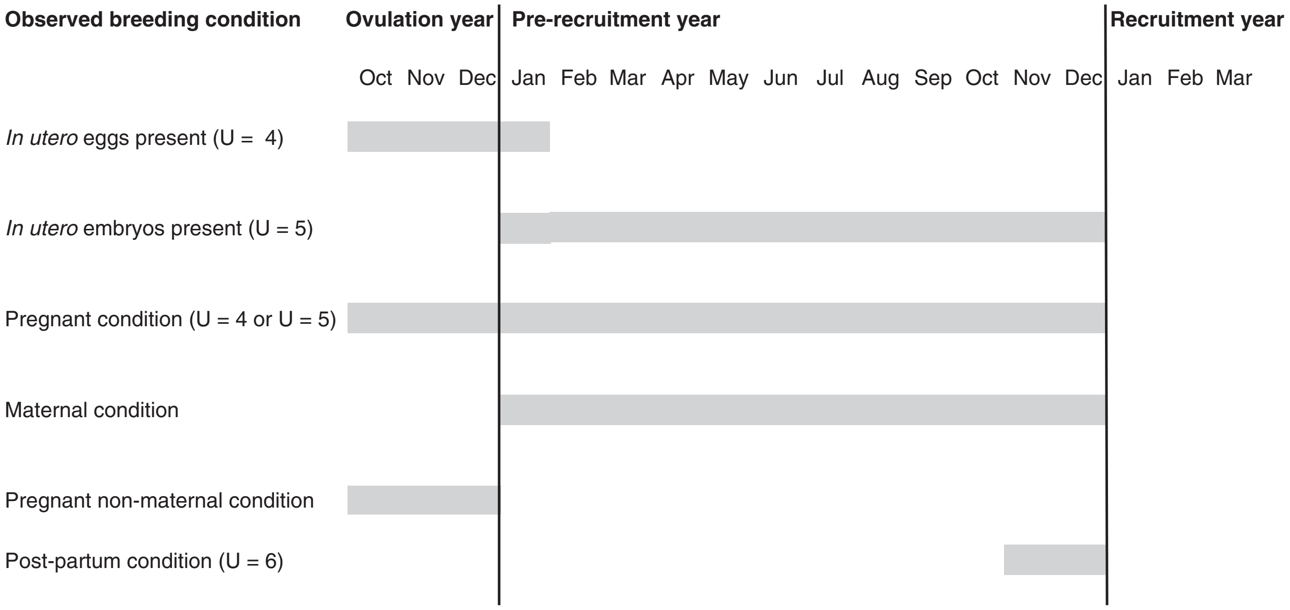

Fig. 12. Synchrony of breeding condition in *Mustelus antarcticus* females. The U = 6 condition can occur at any time, but only data from November to December is included for maternal condition. In Western Australia, U = 4 females are observed from late November to early February and U = 5 females are observed from January to December of pre-recruitment year; full-term embryos are observed from January to early March of recruitment year (Lenanton *et al.* 1990).

granulosus were demonstrated by Ranzi (1932) by way of three separate measurements expressed as a percentage of their total wet mass. These were mass of water (46.2% in eggs and 76.0% in embryos), dry mass of organic material (52.6% in eggs and 20.5% in embryos) and dry mass of inorganic material (1.1% in eggs and 3.5% in embryos). Such reported values vary among species and are prone to marked measurement error (Hamlett *et al.* 2005*b*). A small number of measurements from *M. antarcticus* indicated a 377% increase in total dry mass from egg to mid-term embryo, and a 784% increase from egg to full-term embryo (Storrie 2004). Irrespective of type of measurement, the comparatively small size of *M. antarcticus* eggs indicates that the species exhibits matrotrophic aplacental viviparity with histotrophy. The embryos are nourished by uterine secretions in addition to comparatively low yolk sac reserves (Storrie 2004). Conversely, *C. granulosus*, which has ripe ovarian follicles that reach a wet mass of >350 g (Guallart and Vicent 2001), exhibits lecithotrophic aplacental viviparity, whereby the embryos are completely or mostly nourished by yolk sac reserves (Hamlett et al. 2005*b*).

Period of ovarian cycle

For viviparous chondrichthyan species, the period of the ovarian cycle is defined here as the period from completion of sequential ovulation of one series of oocytes to completion of sequential ovulation of the next series of oocytes. Apart from females approaching first ovulation, ovulation normally follows parturition. As with pregnancy within a population, the ovarian cycle of most species is generally synchronous, with some variation in timing among individual mature females. Most species reported with an annual cycle inhabit depths of <300 m, but there are exceptions with asynchronous cycles, such as *S. megalops* (Braccini *et al.* 2006). The period of ovarian cycles in species found at greater depths are less certain, but are generally asynchronous and longer than one year. For a female with an annual cycle that is experiencing first pregnancy, the period from when the oocytes in the follicles begin yolking to the time of complete ovulation, together with the period of gestation, is ~two years for many species. For subsequent pregnancies, vitellogenesis mostly proceeds concurrently with gestation, and thus parturition can occur annually. Examples of shark species with annual cycles include *M. mustelus* (Smale and Compagno 1997), *M. canis* (Conrath and Musick 2002), *M. manazo* (Yamaguchi *et al.* 2000), *Carcharhinus tilstoni*, *Carcharhinus sorrah* (Stevens and Wiley 1986), *Carcharhinus acronotus* (Hazin *et al.* 2002) and *R. terraenovae* (Loefer and Sedberry 2003). The highest reported LFDs at ovulation for species with annual ovarian cycles are mostly <30 mm. For species in which the ovarian cycle is biennial, such as *S. acanthias* (Hanchet 1988) and *S. megalops* (Braccini *et al.* 2006), or triennial, such as *G. galeus* (Walker 2005), LFD reaches >40 mm. Species found at depths of <300 m with follicles that attain larger sizes include the squatinids such as *Squatina tergocellata* (68 mm LFD) (Bridge *et al.* 1998), *Squatina squatina* (86 mm) and *Squatina oculata* (74 mm) (Capapé *et al.* 1990). These squatinid species appear to have ovarian cycles of two or three years (Capapé *et al.* 1990). Squalid species inhabiting continental slopes, such as *Centroscymnus owstoni*, *Centroscymnus coelolepis*, *Centrophorus squamosus* and *Centrophorus granulosus*, also have large follicles (60 to 87 mm diameter) (Yano and Tanaka 1988; Girard and Du Buit 1999; Guallart and Vicent 2001) and may have asynchronous ovarian cycles with periods exceeding three years. Asynchrony in the ovarian cycle of *S. megalops* off southern

Australia (Braccini *et al*. 2006) appears consistent with the pattern among continental-slope squalids, despite occurring mostly in coastal waters; *S. acanthias* is a notable exception (Hanchet 1988). Protracted egg-laying periods in many oviparous species also make for indistinct periodicity in the ovarian cycle, e.g. *Galeus eastmani* and *Galeus nipponensis* (Horie and Tanaka 2000).

Mustelus antarcticus is one of only two chondrichthyan species reported to exhibit ovarian cycles with different periods in separate regions. However, it is not surprising that there were several exceptions to the annual ovarian cycle in WKI and to the biennial ovarian cycle in EKI. First, it is unlikely that there is a distinct boundary between the females with an annual cycle and those with a biennial cycle: there is likely to be a mixing zone. Second, it is known that there is some movement of the population across southern Australia. Annually, 5% of the population of females of TL > 1100 mm move from the SA region to the BS/Tasmanian regions, and 9% move from the BS/Tasmanian regions to SA (see Fig. 1). Furthermore, it is estimated that 3% move from Western Australia to SA and 9% from SA to Western Australia (Walker *et al*. 2000). Hence, it is expected that some females on an annual ovarian cycle will move from WKI to EKI and that some females on a biennial cycle will move from EKI to WKI. Marked environmental differences between WKI and EKI (see 'Materials and methods') is a likely explanation for the difference in the period of the ovarian cycle between these two regions.

Mustelus manazo is the other chondrichthyan species reported to have regionally different ovarian cycles. This species has an annual ovarian cycle, and hence annual parturition, over most of its range, but there is evidence of a biennial ovarian cycle in the Aomori region of Japan where water temperature is lowest (Yamaguchi *et al*. 2000). This suggests that the frequency of parturition is limited by the period of the ovarian cycle, and that vitellogenesis occurs more rapidly in warmer water than cool water. Such a response to water temperature might explain why the females of highly migratory species, such as *G. galeus* (Walker 2005) and *Prionace glauca* (Nakano 1994), tend to move to warmer regions during the cool months of the year, while the males remain in cooler waters. This might also explain why species inhabiting the deep cold waters of the world's continental slopes mostly have ovarian cycles of two or more years.

Length-at-maturity and length-at-maternity

The pattern of differences evident in *M. antarcticus* from EKI among the periods 1973–76, 1986–87, and 1998–01 are generally similar for ogives of TL-at-maternity and for female and male ogives of TL-at-maturity. TL-at-maturity and TL-at-maternity mostly increased (ogives moved right) between 1973–76 and 1986–87 and then decreased (ogives moved left) between 1986–87 and 1998–01; the one exception is female TL-at-maturity, which did not decrease between 1986–87 and 1998–01. The difference in female and male TL-at-maturity between WKI and EKI is that WKI 1986–87 is similar to EKI 1973–76 for females and similar to EKI 1986–87 for males. There is good agreement visually between the pregnancy ogive for Western Australia (Lenanton *et al*. 1990) and the maternity ogive for WKI (present study), but the comparison cannot be readily statistically tested. Too few small immature sharks were collected during the Western Australian study to facilitate comparisons based on female and male maturity.

The observed patterns of differences in TL-at-maturity and TL-at-maternity, determined from data collected by several observers, are unlikely to be markedly affected by the observer. Classing females for maturity or maternity is less subjective than classing males for maturity. Classing females as either mature or immature from measurements of LFD is objective and does not require subjective judgement on the part of the observer. Classing females as either maternal or non-maternal from uterus condition might have a small observer-effect. Distinguishing between uterus conditions U = 6 and U = 3 in some females can be subjective because, following parturition, the distended appearance of uterus condition U = 6 gradually changes to the non-distended appearance of condition U = 3. The classification of males for maturity from clasper calcification or from testis development is the most subjective, and could vary among observers. Macroscopic inspection of seminal vesicle condition is the least subjective of the macroscopic methods; however, there can be some uncertainty distinguishing between the immature (V = 1) and the spent condition (V = 3) in some males. Spermatogenesis staging is the least subjective of all four methods for males, but the method has the disadvantage of being highly labour intensive owing to its requirement for laboratory preparation, whereas all three macroscopic methods can be undertaken rapidly in the field.

The patterns of difference in TL-at-maturity and TL-at-maternity of *M. antarcticus* between the regions west and east of Kangaroo Island might be partly explained by differing environmental conditions such as water temperature (see 'Boundaries of regions for statistical analysis'). *Mustelus manazo* matures at a smaller size in the southern region (Taiwan) than in the more northerly region (Japan) of its distribution, suggesting that females and males mature at smaller sizes in warmer waters (Yamaguchi *et al*. 2000). Differences in seasonality and food availability are suggested causes of differences in size-at-maturity and other reproductive variables of *Sphyrna tiburo* between two localities in Florida (Parsons 1993). However, the patterns of change in TL-at-maturity and TL-at-maternity of *M. antarcticus* among the sampling periods 1973–76, 1986–87 and 1998–01 observed in the present study are not readily explainable by environmental change.

The patterns of change in TL-at-maturity and TL-at-maternity among the three sampling periods for *M. antarcticus* are contrary to those expected from a density-dependent response to a change in population abundance. As the population in EKI declined between 1973–76 and 1986–87 with rising fishing mortality (Walker 1994), TL-at-maturity and TL-at-maternity increased rather than decreased, as would be expected from a density-dependent response. Similarly, as the population increased between 1986–87 and 1998–01 with falling fishing mortality, TL-at-maturity and TL-at-maternity mostly decreased rather than increased as might be expected. Clearly, if density-dependent responses did occur, they were completely masked by other effects. Various mechanisms have been proposed for density-dependent regulation in shark populations such as *S. acanthias* when the population size becomes reduced. (1) Compensatory decreases in natural mortality result from decreased predation, cannibalism, competition or disease. (2) Compensatory increases in fecundity occur when food is more readily available or when foetal mortality decreases. (3) Compensatory increases in growth rate occur when abundant food induces earlier maturity and greater fecundity for each age-class (assuming that fecundity and maturity are related to size rather than age) (Holden 1973). On the north-eastern coast of the USA, there is evidence that l_{50} increased with increasing stock abundance (Silva 1993) and subsequently decreased with decreasing stock abundance from 1998 to 2002 (Sosebee 2005).

The observed patterns of change in TL-at-maturity and TL-at-maternity among the three sampling periods for *M. antarcticus* are better explained by the effects of length-selective fishing mortality than by the effects of density-dependent responses. Gill-nets of 6 to 7-inch mesh size used in the shark fishery off southern Australia are most effective at catching mid-sized sharks; small sharks swim through the meshes, whereas large sharks tend to deflect from the gill-nets because their heads cannot penetrate the meshes. This has the effect of selectively removing large young sharks and small old sharks from the population of *M. antarcticus*. Furthermore, a fast-growing individual has a higher probability of survival than does a slow-growing individual, because the period of exposure to high selectivity is shorter for a fast-growing individual than for a slow-growing individual. Sampling length-at-age data from a population where the length distribution-at-age has been distorted by the effects of length-selective fishing gives rise to the 'phenomenon of apparent change of growth rate' (Walker *et al.* 1998). This is reflected in distortions to the shape of growth curves produced from the length-at-age data (Lee 1920; Ricker 1969). If maturity and maternity relate to age, as well as to TL, such changes in the population will similarly distort the shape of maturity and maternity ogives to produce apparent rather than real changes in TL-at-maturity and TL-at-maternity. The general pattern of TL-at-maturity and TL-at-maternity increasing from 1973–76 to 1986–87 and decreasing from 1986–87 to 1998–01 is consistent with length-selective fishing mortality as the cause of an apparent change rather than a real change. In EKI, commercial gill-net fishing effort approximately tripled from 1973–76 to 1986–87 and subsequently halved from 1986–87 to 1998–01. Differences in fishing effort and differences in mesh-size of commercial gill-nets deployed between regions might also explain some of the difference in the shape of the ogives between WKI and EKI during 1986–87. In EKI, most gill-nets had a 7-inch mesh size during 1973, but this changed rapidly to a mostly 6-inch mesh size by 1976. Since then, most gill-nets were of 6-inch mesh size, apart from small numbers of 6.5-inch mesh size that were used mainly in the western-most regions of EKI. In WKI, most gill-nets were of 7-inch mesh size during and between the periods 1973–76 and 1986–87, with some use of gill-nets of 8-inch mesh size during the early part of this period.

The hypothesis for the 'phenomenon of apparent change of growth rate' (term coined by Lee 1920) caused by length-selective fishing mortality from gill-nets was invoked to explain differences in the von Bertalanffy growth curves of *M. antarcticus* between 1973–76 and 1986–87 in BS and between BS and SA during 1986–87 (Walker *et al.* 1998). Similarly, length-selective fishing mortality is the most likely hypothesis to explain marked differences in the shape of TL-at-maturity and TL-at-maternity ogives among the periods 1973–76, 1986–87 and 1998–01 in EKI, observed in the present study. Hence, I invoke the hypotheses for the 'phenomenon of apparent change of size-at-maturity' and 'phenomenon of apparent change of size-at-maternity' caused by length-selective fishing mortality from gill-nets to explain the differences in various ogives found during the present study. If length-selective fishing mortality can have marked biasing effects on von Bertalanffy growth curves and maturity and maternity ogives, it follows that the most reliable relationships to use for demographic analysis or fishery stock assessment are those determined when fishing mortality is lowest. For *M. antarcticus* this is for the relationships determined from data collected during 1973–76.

The marked effect of length-selective fishing mortality causing an apparent rather than real increase in TL-at-maturity can be shown for *M. antarcticus* from two von Bertalanffy growth curves whereby the phenomenon of apparent change of growth rate was demonstrated (Walker *et al.* 1998). This involves taking a single known TL-at-maturity relationship and expressing the proportion of population in mature condition against age (i.e. age-at-maturity ogive) by substituting for TL in each of the two von Bertalanffy growth curves. The growth curves considered are for each of females and males in BS during 1973–76 and 1986–87 (Moulton *et al.* 1992), re-designated to EKI. Thus, for each sex, I take an EKI 1973–76 TL-at-maturity relationship and combine it with each of the von Bertalanffy relationships for EKI 1973–76 and EKI 1986–87. Both the resulting female and male age-at-maturity ogives are shifted markedly to the right from 1973–76, when fishing mortality with gill-nets was low, to 1986–87, when fishing mortality with gill-nets was high (Fig. 13). The same effect can be demonstrated for TL-at-maternity.

Most studies determine maturity ogives, but fail to determine maternity ogives, and various studies have defined maturity very differently (Conrath 2005; Walker 2005). Use of maturity ogives instead of maternity ogives in demographic analysis or fishery stock assessment is likely to overestimate predicted recruitment from these models, leading to bias in the assessments (Walker 2005; Braccini *et al.* 2006). Where parturition is annual, this bias is not as serious as it is for species that have longer parturition cycles.

Seasonal variation in male breeding condition

There are no documented observations of *M. antarcticus* mating, but inferences on the timing of copulation can be made from the seasonality of the female breeding cycle, male GSI, seminal vesicle fullness and spermatozoa production from spermatogenesis. The presence of fresh courtship scars on adult females has been used to establish the time of mating in other species (Pratt and Carrier 2005), but neither fresh nor healed scars were observed on *M. antarcticus*. Frequent observations of predominantly male or predominantly female sharks caught at individual fishing sites during sampling operations suggest the sexes are often separate. At one such site in the Great Australian Bight on 1 November 1995, many of the mature males had copious seminal fluids on their claspers, providing evidence that males west of Kangaroo Island were ready to mate during the peak season for female parturition and ovulation. However, east of Kangaroo Island,

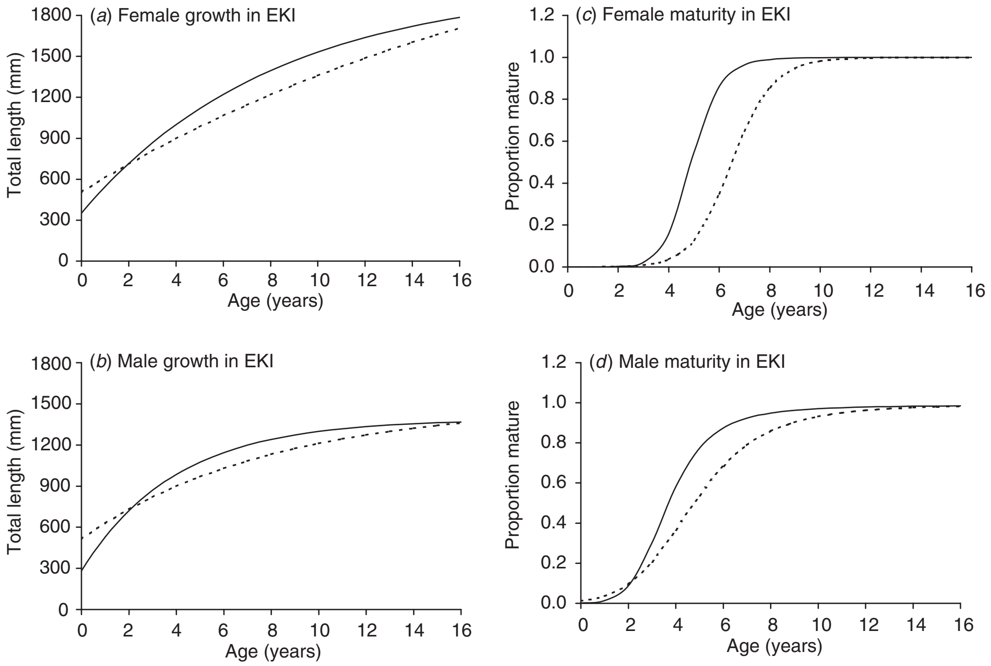

Fig. 13. TL- and maturity-age to illustrate 'phenomenon of apparent change in size-at-maturity'. Von Bertalanffy growth curves for (*a*) females and (*b*) males and maturity-age curves for (*c*) females and (*d*) males during 1973–76 (——) and 1986–87 (- - - - -) in EKI. The growth curves were generated from parameters reported by Moulton *et al.* (1992), and the TL-at-maturity curves were generated from parameters determined from the present study. Female TL-at-maturity was obtained from EKI 1973–76 (see Fig. 9*a*) and male TL-at-maturity was obtained from seminal vesicle condition from EKI 1973–76 (see Fig. 10*a*).

female (including pregnant) *M. antarcticus* with spermatozoa detected in the uterine sphincter or oviducal gland (or both) were collected at various times of the year (Storrie 2004), which is consistent with either protracted mating or a seasonal mating season followed by an extended period of sperm storage.

Fertilisation in chondrichthyans occurs as each ovum passes through the oviducal gland, most likely from sperm stored in the terminal zone of the oviducal gland from past matings (Hamlett *et al.* 2005*a*). During pregnancy, uterine eggs or embryos and, as in *M. antarcticus*, intrauterine compartments probably obstruct passage of spermatozoa – received by insemination through the uterine sphincter – from reaching the oviducal glands. Hence, for species such as *M. antarcticus* from WKI or Western Australia that have an annual female breeding cycle, spermatozoa may only successfully pass through the uteri to the oviducal glands during the brief period from the end of parturition to the beginning of the next ovulation. However, for those with a biennial or triennial female breeding cycle, there is a ~1 to 2-year period from the end of parturition to the beginning of next ovulation when insemination can occur. For *M. antarcticus* distributed west of Kangaroo Island, unless all or most insemination occurs before a female's first ovulation and sperm can be stored for several years, it follows that the male breeding cycle must be closely synchronised with the female breeding cycle to ensure effective insemination before the start of ovulation. Conversely, the need for such synchronisation between the male and female breeding cycles east of Kangaroo Island is not essential because insemination and replenishment of sperm in the oviducal glands can occur over a full year. This difference in the need for synchrony between sharks distributed east and west of Kangaroo Island might explain some of the seasonal differences in the male breeding condition between these two broad regions found in the present study and the Western Australian study (Lenanton *et al.* 1990).

In Western Australia, there is a clear pattern of seasonality in male testis index (Lenanton *et al.* 1990), which relates to GSI. Data from that study, together with the small amount of GSI data from the present study obtained from WKI (Fig. 11*d*), exhibit the pattern of a gradual increase in GSI from February to September, a rapid decrease during October, and a stabilisation at this lower level between November and February for the broad region west of Kangaroo Island. The pattern of spermatozoa production from spermatogenesis in EKI (Fig. 11*b*) is similar to the trend in GSI west of Kangaroo Island, particularly the gradual increase from February to September, but it remains steady between September and December before declining rapidly. Trends in seminal vesicle fullness appear to be similar between WKI and EKI, apart from mostly higher values in WKI than in EKI; however, no data were collected from WKI between December and March. Seminal vesicle fullness is low between April and August and high between September and November in both WKI and EKI, and remains high between December and March in EKI. What is remarkable is that there is no trend in the GSI of sharks EKI, whereas there are strong trends in GSI and seminal vesicle fullness of males from WKI and in spermatozoa production and seminal vesicle fullness of males from EKI. The present study provides no evidence that the weak seasonal trend in the HSI of sharks from EKI relates to male breeding condition.

The pattern of peak GSI in males before ovulation in females (in the present study, observed in female *M. antarcticus* collected west of Kangaroo Island) is also commonly observed among other chondrichthyan species, e.g. *Carcharhinus cautus*, *C. melanopterus* and *C. fitzroyensis* (Lyle 1987). Similarly, the pattern of peak spermatozoa production in male *M. antarcticus* from EKI during September, which is shortly before the beginning of the period of ovulation in females (October), is similar to the patterns reported for other mustelids. Spermatozoa production peaks shortly before ovulation in *M. manazo* and *M. griseus* from Japan (Teshima *et al*. 1974; Teshima 1978) and in *M. canis* from the north-western Atlantic Ocean (Conrath and Musick 2002). There are also clear GSI seasonal cycles in *M. manazo* and *M. griseus*, but these are out of phase with peak spermatozoa production by several months (Teshima 1978), thus differing from *M. antarcticus*, which shows that spermatozoa production in EKI is in phase with GSI in the broad region west of Kangaroo Island.

Most species of *Mustelus* breed annually (see above), suggesting that female *M. antarcticus*, or an ancestral species, had an exclusively annual breeding cycle – as displayed west of Kangaroo Island – that has adapted to provide a more flexible breeding cycle to allow distribution within a broader range of environmental conditions throughout southern Australia. The species may have also varied its male breeding cycle from one that is highly seasonal to include one that is more protracted. Although spermatozoa production peaks shortly before ovulation begins, spermatozoa are produced at all times of the year (Fig. 11*b*), and some males are observed with full seminal vesicles at most times of the year. A highly seasonal male breeding cycle west of Kangaroo Island and a protracted male breeding cycle east of Kangaroo Island might also explain GSI seasonality west and lack of GSI seasonality east of Kangaroo Island. Interestingly, *M. manazo* males exhibit a similar pattern, whereby there is distinct seasonality in GSI in regions where the females have annual ovarian and parturition cycles and a lack of seasonality in GSI where the females have biennial ovarian and parturition cycles (Yamaguchi *et al*. 2000).

Summary

Eighteen summary points are provided on the reproductive biology of *M. antarcticus* across southern Australia.

(1) Maximum TL is longer in females (1852 mm) than in males (1482 mm), and maximum total body mass of females (24.8 kg) is almost double that of males (13.5 kg). At any TL > 700 mm, the mean total body mass of females is higher than that of males.

(2) The number of embryos *in utero* per pregnant female ranges from 1 to 57 and increases curvilinearly with maternal TL. The relationship between the number of *in utero* embryos and maternal TL differs between west and east of Kangaroo Island, but does not differ with sampling period.

(3) The sex ratio of embryos is 1:1, and the number of embryos in the left uterus equals the number in the right uterus. Of eggs *in utero*, 93.2% develop as embryos, whereas 6.8% remain infertile. However, the number of infertile eggs in the left uterus is higher than the number in the right uterus of pregnant females.

(4) Ovarian follicle diameter ranges from 15 to 28 mm at ovulation, and ovary mass reaches 282 g in preovulatory females and 195 g in pregnant females carrying embryos close to full-term. Ovary mass is mostly <70 g in females at all other stages of maturity. A positive correlation between HSI and LFD indicates that liver mass increases during the process of vitellogenesis. The highest HSI occurs in ovulating females, which suggests that liver mass and presumably its lipid content increase in preparation for pregnancy.

(5) Ovulation occurs from October to January (predominantly from November to December) east of Kangaroo Island; the period is likely to be similar west of Kangaroo Island.

(6) The ovarian and parturition cycles are seasonal and synchronous with up to 3 months variation among individual females. These cycles are predominantly annual west of Kangaroo Island and predominantly biennial east of Kangaroo Island; this difference coincides with environmental differences between these broad regions.

(7) Males exhibit seasonality in breeding condition, but the timing of copulation is uncertain east of Kangaroo Island. There are strong seasonal trends in male GSI and seminal vesicle fullness that coincide with female ovulation and parturition west of Kangaroo Island, and in spermatozoa production and seminal vesicle fullness east of Kangaroo Island, but there is no trend in GSI east of Kangaroo Island.

(8) Embryos in pregnant females grow from January to December, indicating that the period of gestation throughout southern Australia is ~1 year. There is synchrony in the growth of embryos both within and between the regions west and east of Kangaroo Island. Parturition is mostly complete by the end of December.

(9) There is a 10-fold gain in mean wet mass from eggs (10 g) to full-term embryos (~100 g) of ~330 mm TL. The wet mass of external yolk sacs depletes rapidly during the early stages of gestation, and even though *M. antarcticus* exhibits aplacental viviparity, there must be sources of nutrients available for embryonic growth additional to those provided from the yolk sac.

(10) The mean wet mass of infertile eggs persisting *in utero* throughout gestation (9.9 g) is similar to the mean wet mass of eggs *in utero* soon after ovulation (10.0 g).

(11) Results obtained for maturity depend on explicit definitions of terms. A definition of female maturity based on the diameter of the largest ovarian follicle provides an objective criterion unlikely to be affected by field observer. However, a definition of male maturity is more problematic in that all methods require a degree of judgment by the observer. The seminal vesicle condition and stage of spermatogenesis methods are less subjective than the testis development and clasper calcification methods.

(12) A female *M. antarcticus* is in maternal condition if, assuming it had survived, it would have contributed to recruitment by 1 January (i.e. end of gestation and beginning of the recruitment year). A definition of maternity based on uterus condition provides objective criteria unlikely to be affected by the field observer, other than occasional uncertainty distinguishing between uterus conditions U = 3 and U = 6.

(13) The patterns of difference between regions east and west of Kangaroo Island during 1986–87 and patterns of change east of Kangaroo Island among periods 1973–76, 1986–87 and 1998–01 are similar for female TL-at-maturity and TL-at-maternity, with one notable exception. East of Kangaroo Island, the TL-at-maternity ogive increases from 1973–76 to 1986–87, but reduces to approach the 1973–76 level from 1986–87 to 1998–01. The TL-at-maturity ogive follows a similar pattern with the exception that it is larger during 1998–01 than during 1986–87. The 1986–87 maturity ogive for the region west of Kangaroo Island lies between the 1973–76 and 1986–87 ogives for the region east of Kangaroo Island; the maternity ogives cannot be readily compared because $P_{\mathrm{Max.}(l)} = 1.00$ west of Kangaroo Island, whereas $P_{\mathrm{Max.}(l)} = 0.50$ east of Kangaroo Island.

(14) Male seminal vesicle condition, testis development, and spermatogenesis staging give similar estimates of TL-at-maturity, whereas clasper calcification gives higher TL-at-maturity estimates than the other three methods. East of Kangaroo Island, the TL-at-maturity ogive increases from 1973–76 to 1986–87, but decreases to approach 1973–76 values from 1986–87 to 1998–01. The male maturity ogive is steeper for 1986–87 and 1998–01 than for 1973–76. The 1986–87 TL-at-maturity ogives are similar between regions west and east of Kangaroo Island.

(15) The patterns of TL-at-maturity are mostly similar between males and females for the three periods, with one notable exception. West of Kangaroo Island during 1986–87, TL-at-maturity was similar to 1973–76 for females east of Kangaroo Island, and similar to 1986–87 for males east of Kangaroo Island. This suggests that the effect of length-selective fishing mortality (from gill-nets of predominantly 7-inch mesh size) on males is stronger than that on females west of Kangaroo Island. This is because large females have a higher probability of escaping the nets than the large males, which have a smaller maximum size.

(16) The 'phenomenon of apparent change of size-at-maturity' and 'phenomenon of apparent change of size-at-maternity' caused by length-selective fishing mortality by gill-nets are invoked as hypotheses to explain the patterns of differences in TL-at-maternity and TL-at-maturity ogives among sampling periods. Some of the differences between regions west and east of Kangaroo Island might be explained by these hypotheses, but environmental differences are likely to contribute. Any density-dependent responses to changes in population size (owing to fishing effort) that might be reflected in these ogives are completely masked by the effects of gill-net length-selective fishing mortality.

(17) The most reliable estimates of TL-at-maternity ($l_{50} =$ 1129 mm, $l_{95} = 1344$ mm and $P_{\mathrm{Max.}} = 0.500$) and female TL-at-maturity ($l_{50} = 1105$ mm, $l_{95} = 1293$ mm and $P_{\mathrm{Max.}} =$ 1.000) are expected to be those from east of Kangaroo Island during 1973–76. These estimates are based on large sample sizes and are relatively free of the biasing effects of gill-net length-selective fishing mortality, which was lowest during 1973–76. The only estimates from west of Kangaroo Island for TL-at-maternity ($l_{50} = 1263$ mm, $l_{95} = 1523$ mm and $P_{\mathrm{Max.}} = 1.000$) and female TL-at-maturity ($l_{50} = 1129$ mm, $l_{95} = 1392$ mm and $P_{\mathrm{Max.}} = 1.000$) were obtained during 1986–87. However, these estimates are likely to be biased upwards owing to the effects of length-selective fishing mortality. The effects of the observer on these estimates are minimal.

(18) The most reliable estimates of male TL-at-maturity from east of Kangaroo Island are most likely those determined from seminal vesicle condition ($l_{50} = 953$ mm, $l_{95} = 1245$ mm and $P_{\mathrm{Max.}} = 1.000$) during 1973–76. These estimates are a little larger than those from microscopic determination of spermatogenesis stage ($l_{50} = 923$ mm, $l_{95} = 1160$ mm and $P_{\mathrm{Max.}} = 1.000$). These estimates are based on large sample sizes and are least influenced by the biasing effects of observer or gill-net length-selective fishing mortality. The most reliable estimates of male TL-at-maturity from west of Kangaroo Island are based on seminal vesicle condition ($l_{50} = 978$ mm, $l_{95} = 1119$ mm and $P_{\mathrm{Max.}} = 1.000$) during 1986–87.

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Reproduction of *Heterodontus portusjacksoni* in Victoria, Australia: evidence of two populations and reproductive parameters for the eastern population

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Abstract. Significant differences in the length–frequency composition of catch samples, mass–length relationships and length-at-maturity found between *Heterodontus portusjacksoni* from western and far-eastern Victoria, suggest the presence of at least two separate breeding populations off south-eastern Australia, with some mixing between these regions. In each region females attain a larger size than males, and collectively those sharks in western Victoria are smaller, present higher mass-at-length, and lower length-at-maturity than those in far-eastern Victoria. These regional differences might be a result of sampling bias, length-selective fishing mortality, environmental conditions, or genetic differences. However, tagging evidence from previous studies and the presence of two bio-geographic provinces in the region support the hypothesis of two separate breeding populations. The essential reproductive parameters for *H. portusjacksoni* population analysis in far-eastern Victoria were determined, using a novel method to estimate fecundity and the ovarian cycle of an egg-laying species. In this region, females have between 6 and 20 pre-ovulatory oocytes (average $= 14$, $n = 29$, standard deviation $= 3.71$) before the reproductive season. The species has an annual reproductive cycle correlated with water temperature, with ovulation starting during late winter to early spring and a ~6 month egg-laying period. The period from the onset of vitellogenesis to ovulation of oocytes is ~18 months.

Additional keywords: chondrichthyans, Port Jackson shark.

Introduction

Fishery stock assessment, ecological risk assessment, and assessment of species extinction risk all require quantitative information on a species' reproductive potential. The key reproductive parameters for these assessment methods include: (*1*) the sex ratio at birth; (*2*) the relationship between maternal age or size and the number of offspring (litter size or number of laid eggs per female); and (*3*) the relationship between the proportion of females contributing to annual recruitment and their age or size (maternity ogive). In some cases, the relationship between the proportion of mature females in the population and their age or size (maturity ogive) is also important. Unfortunately, differences in the reproductive strategies of some chondrichthyan species prevent the determination of some of these reproductive parameters (Walker 2005). For example, litter size can be investigated in viviparous species by counting the number of embryos at a full term stage *in utero*. The same method, however, cannot be applied to egg-laying species because oocytes appear to develop continuously and are laid during a protracted reproductive season or all year around. Thus alternative approaches are necessary, and we have developed a novel approach in this paper.

The Port Jackson shark, *Heterodontus portusjacksoni* (Meyer 1793), is an oviparous demersal species endemic to southern Australia (Last and Stevens 1994). It is commonly caught as by-catch by demersal otter trawl, shark gill-net and shark longline fisheries. In terms of mass and number of individuals, the species is the fifth top chondrichthyan species caught in the shark gill-net and longline fisheries in Bass Strait and South Australia (Walker *et al*. 2005), and the twelfth most important species in the trawl fisheries (Walker *et al*. 2007). However, little is known about the impact of these fisheries on its populations.

Several studies of *H. portusjacksoni* have focussed on the structure of the reproductive tract (Jones *et al*. 2005), reproductive physiology (Jones and Jones 1982; Jones and Lin 1992, 1993), and embryonic development (Rodda 2000). Some information about its reproductive biology off New South Wales (NSW) is available (McLaughlin and O'Gower 1971), but tagging studies (O'Gower and Nash 1978) suggest the presence of more than one breeding population off south-eastern Australia. Such separate populations of *H. portusjacksoni* might correspond to bio-geographic provinces, associated with oceanographic conditions and the distribution of dominant flora and fauna (Knox 1963). The aim of the present study was to investigate potential population differences by comparing length–frequency distributions, length–mass relationships and reproductive parameters, such as length-at-maturity, for

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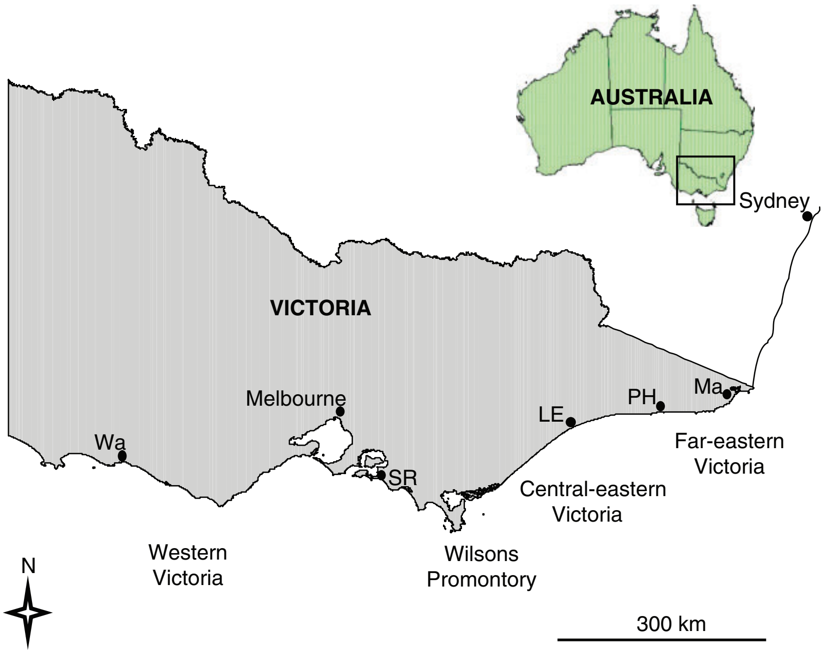

Fig. 1. Fishing ports sampled and regions adopted for *Heterodontus portusjacksoni*. LE, Lakes Entrance; Ma, Mallacoota; PH, Point Hicks; PPB, Port Phillip Bay; SR, San Remo; Wa, Warrnambool.

H. portusjacksoni from three broad regions off Victoria, and to determine the essential reproductive parameters required for population analysis for the putative population in far-eastern Victoria.

Materials and methods

Data collection

A total of 722 *Heterodontus portusjacksoni* was collected (355 females and 367 males) from commercial catches landed in several fishing ports in Victoria, Australia. Samplings were carried out monthly during August 2002–December 2004 and capture methods included demersal otter trawl (mainly in western Victoria), gill-nets and longlines (mainly in eastern Victoria) in depths up to ~80 m. The sharks were kept on ice after capture and transported to the laboratories of Primary Industries Research Victoria in Queenscliff, Victoria, where they were measured, weighed and dissected. Total length (TL) was measured to the nearest 1 mm as a straight line from the tip of the snout to the distal end of the tail, while allowing the shark to take a natural position without being stretched. Total body mass (TW) was obtained using a spring balance (±25 g). Usually there was negligible material in the gut, so stomach content mass was ignored.

Sex and regional comparisons of length, mass and maturity

Preliminary analysis of the data indicated regional differences among some of the relationships between biological variables, such as maturity condition and TL. Hence, data were grouped and analysed separately for three regions designated as: western Victoria (Warrnambool, Port Phillip Bay and San Remo; 21% of samples), central-eastern Victoria (Lakes Entrance; 17% of samples), and far-eastern Victoria (Point Hicks and Mallacoota; 62% of samples) (Fig. 1) to coincide with the two bio-geographic provinces and an overlapping zone (Knox 1963). However, regional comparison was not undertaken for other reproductive relationships, such as those for fecundity and TL, and the ovarian and reproductive cycle of *H. portusjacksoni*, because they could not be determined in western and central-eastern Victoria where only small numbers of mature sharks were collected during each month. Such information is presented only for far-eastern Victoria, where sampling was more intense, allowing estimation. Owing to sexual dimorphism in size, regional analysis was undertaken for each sex separately. Length–frequency distributions were compared among the regions using χ^2 tests.

The power model $TW = acTL^b$ was used to describe the relationships between TW and TL. In this equation c is a factor correcting for the effects of logarithmic transformation of the data (Beauchamp and Olson 1973), and a and b are parameters estimated for the linear regression equation $ln(TW) = a + b\,ln(TL)$. Differences in this relationship among regions for $ln(TL)$ and their interaction in $ln(TW)$ were tested by analysis of covariance (ANCOVA) using the generalised linear model $ln(TW) = c' + Rg + ln(TL) + Rg \times ln(TL) + \epsilon$, where c' is constant, Rg is the region factor, $ln(TL)$ is a covariate, and $Rg \times ln(TL)$ is an interaction term. Stepwise backward elimination was used to determine the significant terms in this model. Non-significant interactions and then other non-significant terms ($P > 0.05$) were sequentially excluded from the model, until only significant terms remained (Walker 2005, 2007).

Table 1. Maturity indices for *Heterodontus portusjacksoni* using the condition of reproductive structures

Maturity condition	Females			Males		
	Ovaries	Oviducal glands	Uteri	Testis	Claspers	Seminal vesicles
1) Immature	Undifferentiated from the epigonal organ, without visible oocytes	Indistinct from anterior oviduct	Indistinct from anterior oviduct	Undifferentiated from the epigonal organ	Short and non-calcified	Thin strip with translucent walls
2) Maturing	Whitish oocytes ≤3 mm in diameter	Differentiated from anterior oviduct, longer than wider	Narrow tubulus	Differentiated from the epigonal organ, neither lobular nor vascularised	Elongated and partly calcified	Thin strip with translucent walls
3) Mature	Vitellogenic (yellowish) oocytes >3 mm in diameter	Heart shaped, wider than longer	Narrow tubulus, with eggs or distended walls	Elongated, lobular and vascularised	Elongated and fully calcified	Thickened opaque walls, with or without seminal fluids

The ANCOVAs were undertaken by using the general linear modelling (GLM) procedure of the SAS statistical software package (SAS Institute, North Carolina, USA). Comparison between the sexes was carried out to explore potential differences in mass at any given length using a similar model.

Female maturity was assessed using three indices based on macroscopic examination of the ovaries, oviducal glands and uteri (Table 1). Females were considered as mature if their ovaries had vitellogenic oocytes >3 mm in diameter, as this represents the approximate time of the onset of vitellogenesis in other species (Walker 2005, 2007). The length and width of the oviducal glands, as well as the length and width at the central regions of the uteri, were measured to the nearest 1 mm using callipers. Male maturity was assessed using three indices based on macroscopic examination of the testis, claspers and seminal vesicles (Table 1). Clasper length (CL) was measured to the nearest 1 mm, from the join in the skin near the pelvic fin to the distal end of the clasper, and plotted against the TL of the shark.

Length-at-maturity ogives for each sex were determined using each maturity index separately. However, oviducal glands and uteri indices did not produce good shaped ogives, therefore only those based on gonad index are presented for females. The ogives were determined by applying logistic regression to the proportion of mature sharks (P) as a function of TL in the equation $P = c/[1 + e^{-(a+b\,TL)}]$, where P is given by a random dichotomous variable taking the value of 1 for mature animals and the value of 0 for immature animals, and, a, b and c are parameters. This equation was reformulated to express the relationship in terms of more biologically meaningful parameters as $P = P_{max}[1 + e^{-ln(19)(L-L_{50}/L_{95}-L_{50})}]^{-1}$, where P_{max} equals c and is the maximum proportion of mature animals, and L_{50} and L_{95} are lengths at which 50% and 95% of the maximum proportion of animals mature respectively. L_{50}, L_{95} and their 95% confidence intervals were estimated using the Probit procedure of the SAS statistical software package.

The effects of region on the relationship between P and TL were tested by logistic regression using the model $P = (n/N) = C + Rg + TL + Rg \times TL$, where n is the number of mature animals and N is the total number of animals, C is a constant and Rg is region (Walker 2005).

Fecundity, and ovarian and reproductive cycles in far-eastern Victoria

The average size of oocytes classed as ovulatory (~40 mm diameter and ~40 g mass) was determined from eggs inside freshly laid egg cases (Rodda 2000; Tovar-Ávila 2006). Oocytes that had reached ~75% of the ovulation size (≥35 mm) before the beginning of the egg-laying period were considered as pre-ovulatory eggs that would be ovulated during the following egg-laying period. Annual fecundity was defined as the number of eggs laid per female per season (year) and was estimated by counting the number of pre-ovulatory oocytes in females caught during the months before the onset of egg-laying. Oocytes showing any degree of atresia were not considered, irrespective of their size, because they were considered as non-ovulated oocytes from previous or current egg-laying seasons. Linear regression analysis was used to determine the relationship between the number of pre-ovulatory oocytes and maternal TL.

Seasonal variation in the reproductive organs was examined by comparing the month of collection with: (*1*) gonadosomatic index (GSI); (*2*) hepatosomatic index (HSI) for mature females and males; (*3*) oviducalsomatic index (OSI) for mature females; and (*4*) fullness of the seminal vesicles for mature males. The liver, gonads and oviducal glands were weighed with an electronic balance (±0.005 g). Gonad mass included the epigonal organ mass because of difficulties in separating these tissues, particularly when the gonads were not fully developed. Each index was then calculated as the mass of the organ divided by total body mass. As the right and left oviducal glands were of similar mass, only the right oviducal gland mass was used to calculate OSI. GSI, OSI and HSI data were multiplied by 100 to derive percentages and avoid small numbers. Seminal vesicle fullness was ranked as 0, 1, 2, 3 and 4 quarters, and converted to values of 0.10, 0.25, 0.50, 0.75 and 1.00 respectively (Y). This method avoided zero to allow data transformation. The decimal values Y were then transformed to $\sqrt{\sqrt{Y}}$. The effects of month and region on GSI, OSI, HSI and seminal vesicle fullness, and the possible effect of shark TL were tested by ANCOVA and stepwise backward elimination (Walker 2005, 2007).

The process of oocyte development from the onset of vitellogenesis to ovulation was examined using two methods. The first method was to examine seasonal trends in oocyte size. The diameters of the ovarian oocytes in the 24 largest follicles were measured to ensure that all possible pre-ovulatory oocytes were included. Oocyte diameter was then plotted against the rank of the follicle for each mature female separately as a line graph. These line graphs were plotted together for each season to identify temporal changes in the size of oocytes and number of pre-ovulatory oocytes. The second method was to plot as a scattergram the maximum oocyte diameter (MOD) against day of year (t). Where females had a full range of oocyte sizes in the ovaries, the oocytes could be grouped into three cohorts. These groups or cohorts included the large pre-ovulatory oocytes (used to estimate fecundity), a second group of intermediate-size oocytes, and a third group of small oocytes (immediately following the onset of vitellogenesis). Two or three cohorts were present depending on the time of the year. t was adjusted to separate females with a MOD associated with each of these cohorts. Hence, adjusted t (t_{adj}) was calculated by adding 730 (two extra years) to t for females in which the largest oocyte cohort (pre-ovulatory oocytes or MOD > 35 mm) was present, and adding 365 (one extra year) to t for females with a medium size oocyte cohort (MOD 16–34 mm). t was not adjusted for females with the smallest oocyte cohort (MOD < 15 mm). For those females having more than one oocyte cohort only the largest was considered for this analysis. Linear regression analysis was used to determine the parameters a and b of the equation $\text{MOD} = a + t_{adj}b$. Only data with $t_{adj} < 942$ were used for the regression analysis to avoid bias caused by the continuous ovulation of the largest oocytes after this date.

The proportion of females with pre-ovulatory oocytes for each month and the average number of pre-ovulatory oocytes of females per month were also related to the ovarian and egg-laying cycles. The presence and diameter of *corpora lutea* and *corpora atretica* in the ovary were recorded and related to the reproductive cycle as well. Because of the difficulty in separating these two structures by their macroscopic characteristics at a certain degree of atresia (Hisaw and Hisaw 1959), only yellowish structures were considered as *corpora atretica*, whereas all flat whitish structures were considered *corpora lutea*.

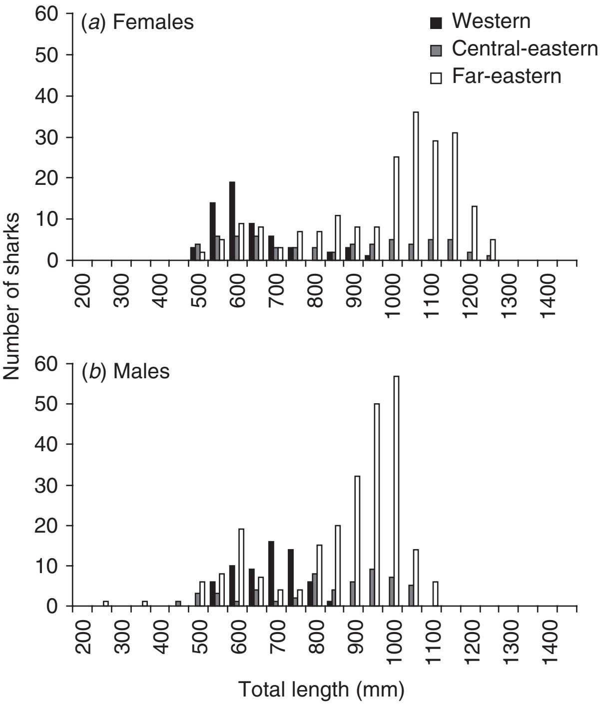

Fig. 2. Length–frequency distribution of *Heterodontus portusjacksoni* (*a*) females and (*b*) males collected in three broad regions off Victoria.

Table 2. Total length (TL) and total body mass (TW) ranges of *Heterodontus portusjacksoni* sampled from each region in Victoria

Region	Females			Males		
	n	TL (mm)	TW (g)	*n*	TL (mm)	TW (g)
Western	60	458–920	750–9100	62	500–816	510–4500
Central-eastern	63	476–1222	700–1450	54	439–1103	650–4150
Far-eastern	207	490–1225	840–1420	244	250–1090	110–9850

Results

Sex and regional comparisons of length, mass and maturity

Significant differences in length–frequency distributions of *Heterodontus portusjacksoni* were found among the three regions for both females ($\chi^2_{30} = 138.92$, $P < 0.0001$) and males ($\chi^2_{30} = 177.07$, $P < 0.0001$) (Fig. 2). Females reached a larger size than did the males in each region, and those sharks of both sexes captured in western Victoria reached a smaller size than those captured in far-eastern Victoria, with a wide range of lengths in central-eastern Victoria (Table 2).

The TW–TL relationships were significantly different between regions for both females (ANCOVA, $F_{2,326} = 7.71$,

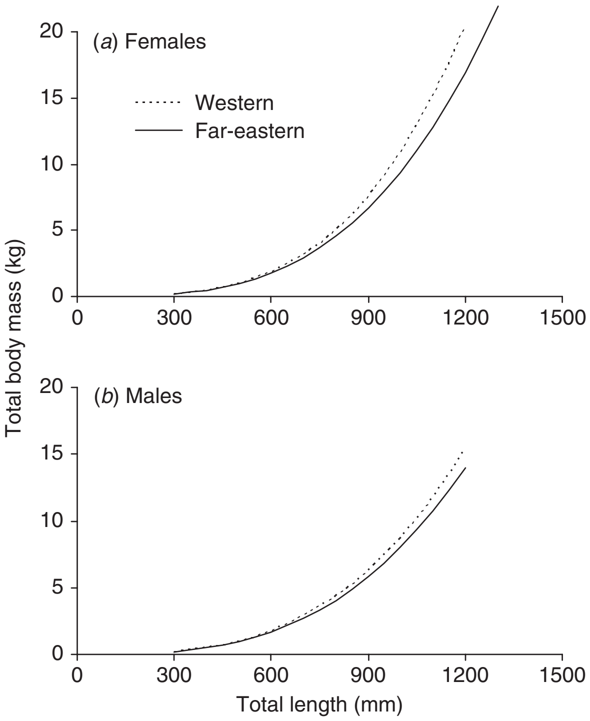

Fig. 3. Relationships between total body mass (TW) and total length (TL) for (*a*) females and (*b*) males from western Victoria (- - - - -) and far-eastern Victoria (——).

$P < 0.0005$) and males (ANCOVA, $F_{2,356} = 10.56$, $P < 0.0001$) indicating mass increases at different rates (Fig. 3). Sharks from western Victoria presented higher mass at any given length than those sharks from far-eastern Victoria, with intermediate mass in central-eastern Victoria (Table 3). Significant differences were also found in the TW–TL relationship between sexes for far-eastern Victoria (ANCOVA, $F_{1,447} = 13.04$, $P < 0.0003$). Sharks of both sexes of *H. portusjacksoni* from all the regions below 600 mm TL presented similar body mass, but differences between females and males and among regions increased with TL. The mass of the heaviest recorded male (10.5 kg, 1050 mm TL) was less than two-thirds the mass of the heaviest female (18 kg, 1210 mm TL).

Mature females had a single functional ovary (right) consisting of oocytes at various stages of development, *corpora lutea* and *corpora atretica* (Fig. 4). The ovary mass of mature females ranged 0.7–6.9% of TW. Mature males had both gonads functional. The testis mass ranged 0.08–1.35% of TW, whereas CL ranged 6.2–13.5% of the TL.

Significant differences in length-at-maturity were found between *H. portusjacksoni* from western and from far-eastern Victoria for each sex (Table 4). Length-at-maturity was smaller in western Victoria than in far-eastern Victoria, with intermediate maturity estimates in central-eastern Victoria. Though maturity ogives in western and far-eastern Victoria presented narrow confidence intervals for both sexes, those from central-eastern Victoria had wide confidence intervals. The relationship between CL and TL showed the same pattern of regional variation. Similar lengths-at-maturity for males were calculated when each of the three maturity indices (claspers, gonads and seminal vesicles) were used (Table 4).

Table 3. Values of parameters and statistical quantities for the equation $TW = ca(TL^b)$ for female and male *Heterodontus portusjacksoni* from each region in Victoria

TW, total body mass; *TL*, total length; *c*, factor correcting for the effects of logarithmic transformation of the data (Beauchamp and Olson 1973); *a* and *b*, parameters; r^2, square of correlation coefficient; *rsme*, root mean square error; *n*, sample size; *P*, probability of statistical significance

Sex and region	*a*	*b*	r^2	*rsme*	*n*	*P*
Females						
Western	4.26 E–10	3.468	0.953	0.0155	60	<0.001
Central-eastern	7.80 E–10	3.308	0.987	0.0122	63	<0.001
Far-eastern	1.71 E–9	3.245	0.972	0.0143	207	<0.001
Males						
Western	3.69 E–9	3.123	0.937	0.0097	62	<0.001
Central-eastern	2.29 E–9	3.181	0.979	0.0125	54	<0.001
Far-eastern	5.52 E–9	3.053	0.978	0.0105	244	<0.001

Fecundity, and ovarian and reproductive cycles in far-eastern Victoria

Reproductively capable females in far-eastern Victoria contained between six and 20 (mean = 14, standard deviation = 3.71, $n = 29$) pre-ovulatory oocytes before the start of the ovulation period. A significant relationship was found between the number of pre-ovulatory oocytes (Y') and maternal TL ($Y' = -14.08TL + 0.0256$, $r = 0.57$, $n = 29$, $P < 0.01$) (Fig. 5).

In this region *H. portusjacksoni* displayed a degree of synchrony in its reproductive cycle, because the start of ovulation and mating (late winter–early spring) and the egg-laying period (late winter–summer) appears to occur at the same time for most of the population based on the analyses of reproductive organs. GSI for mature females increased from summer to autumn (southern hemisphere), peaking during May–June, and decreased during the spring (Fig. 6). In the case of mature males, highly significant differences were detected among months for GSI (ANCOVA, $F_{11,190} = 7.88$, $P < 0.0001$) and seminal vesicle fullness (ANCOVA, $F_{7,153} = 25.18$, $P < 0.0001$). GSI decreased during winter and spring (Fig. 7*a*) and seminal vesicles were full during winter (Fig. 7*b*). The interaction between month and TL was highly significant for both OSI (ANCOVA, $F_{8124} = 5.09$, $P < 0.0001$) and HSI in mature females (ANCOVA, $F_{9,164} = 2.97$, $P < 0.0027$), and for HSI in mature males (ANCOVA, $F_{8,176} = 3.77$, $P < 0.0004$); hence, seasonal variation could not be tested in terms of these indices.

Several cohorts of oocytes were distinguished in the ovary throughout the year. The differences among these cohorts were more evident during winter and autumn (Fig. 8*a*, *d*), when most of the pre-ovulatory oocytes reached the ovulation size. Pre-ovulatory oocytes were found first before the beginning of the ovulation period (autumn). The number of pre-ovulatory oocytes decreased during spring and summer (Fig. 8*b*, *c*), and the sizes of the oocytes of the medium-size oocyte cohort

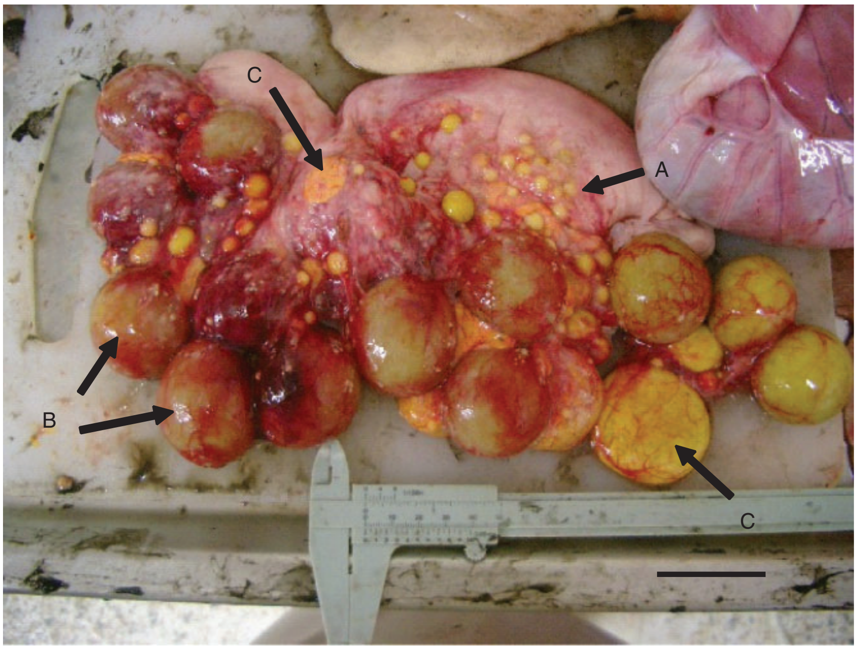

Fig. 4. Mature ovary of *Heterodontus portusjacksoni* showing (A) developing vitellogenic oocytes, (B) pre-ovulatory oocytes and (C) oocytes in different stage of atresia. Scale bar: 40 mm.

Table 4. Mean lengths (mm of total length) at which 50% (L_{50}) and 95% (L_{95}) of the population are mature for female and male *Heterodontus portusjacksoni* from each region in Victoria

CI, 95% confidence intervals; *n*, number of mature animals; *N*, total number of observations; *ML*, maximum likelihood; *P*, probability of statistical significance for differences among regions

Sex	Index	Region	L_{50} (*CI*)	L_{95} (*CI*)	*n*	*N*	*ML*	*P*
Females	Gonad index	Western	858 (812, 933)	1021 (942, 1223)	9	77	−18.706	<0.001
		Central-eastern	919 (854, 978)	1110 (1036, 1287)	26	67	−18.039	<0.001
		Far-eastern	990 (971, 1005)	1178 (1149, 1221)	106	208	−232.967	<0.001
Males	Gonad index	Western	672 (650, 693)	788 (754, 859)	31	71	−47.992	<0.001
		Central-eastern	750 (676, 801)	907 (843, 1112)	25	45	−15.001	<0.001
		Far-eastern	820 (802, 834)	963 (948, 982)	150	231	−249.899	<0.001
	Clasper index	Western	661 (639, 679)	736 (734, 820)	34	71	−43.388	<0.001
		Central-eastern	747 (677, 791)	888 (836, 1027)	36	56	−15.537	<0.001
		Far-eastern	822 (812, 830)	881 (871, 895)	171	243	−80.156	<0.001
	Seminal vesical index	Western	678 (655, 700)	793 (756, 875)	29	68	−43.447	<0.001
		Central-eastern	786 (704, 853)	1031 (937, 1307)	21	45	−21.889	<0.001
		Far-eastern	815 (800, 827)	905 (893, 921)	157	226	−123.344	<0.001

began increasing during spring, and reached ovulation size the following winter (Fig. 8*b*–*d*).

The period from the onset of vitellogenesis to ovulation of oocytes is ~18 months in far-eastern Victoria. A strong relationship was found between the MOD and t_{adj} for sharks from this region ($MOD = -32.2t_{adj} + 0.0835$, $r^2 = 0.74$, $n = 131$, $P < 0.05$) (Fig. 9). The highest proportion of mature females with pre-ovulatory oocytes, and the largest average number of pre-ovulatory oocytes in the ovary was found during autumn–winter (May–August) (Fig. 10). Some females (~25%), however, that had reached L_{50} (955–1077 mm TL) and had expanded uteri and expanded oviducal glands, did not have pre-ovulatory oocytes (10–19 mm of MODs) during autumn–winter as expected. *Corpora lutea* were present throughout the ovulation period, whereas *corpora atretica* were present mainly during summer–autumn, and they increased in number throughout this period. Atresia of a follicle began with the vascularisation of its granulosa and then an increase in its size. These oocytes filled with liquid and then changed their colour and lost the spherical shape to become flattened.

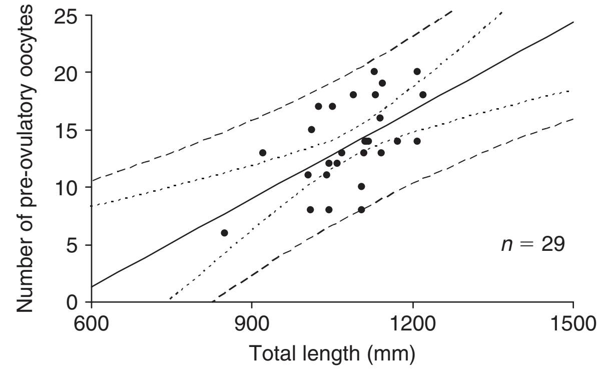

Fig. 5. Relationship between number of pre-ovulatory oocytes and female total length before the egg-laying period (May–June) in far-eastern Victoria. Linear regression (——), 95% confidence limits (– – – –) and 95% prediction intervals (- - - - -) are shown.

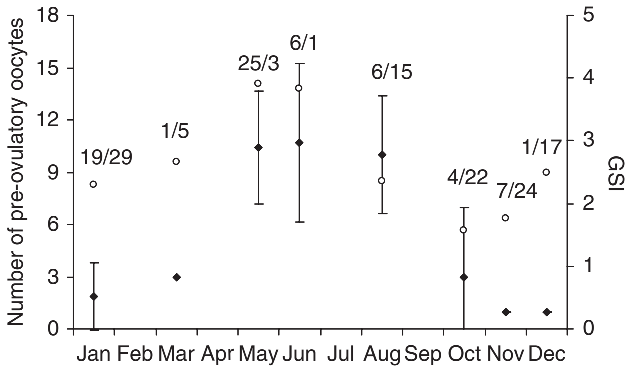

Fig. 6. Mean number of pre-ovulatory oocytes (>35 mm diameter) in the ovary (◆) and average gonadosomatic index (GSI) (○) of mature females from far-eastern Victoria. Standard error bars are shown for number of pre-ovulatory oocytes and the ratios of females with pre-ovulatory oocytes/mature females observed are presented above the bars.

Discussion

Sex and regional comparisons of length, mass and maturity

Sexual dimorphism in the length–frequency distributions, length–mass relationship and length-at-maturity, such as that found for *Heterodontus portusjacksoni* in the present study, is a common feature for many chondrichthyan species; males often reach smaller sizes and mature earlier than females (Ford 1921; Cortés 2000; Walker 2007).

Length-at-maturity ogives for *H. portusjacksoni* are well determined by MOD for females, but indices of oviducal glands and uteri did not produce useful ogives, probably owing to the variation of such structures during the reproductive season. The three male maturity indices provide similar shaped ogives, as has been found in other species (Walker 2005, 2007; Braccini *et al.* 2006).

Estimates of L_{50} in the present study were different from estimates of length-at-maturity in previous studies. In far-eastern Victoria, female and male L_{50} estimates (based on all the three indices used) were considerably higher than length-at-maturity ranges in New South Wales (700–860 mm TL for females based on MOD >9–18 mm; 700–800 mm TL for males based on clasper and testis condition) (McLaughlin and O'Gower 1971), and in another study (Last and Stevens 1994) in which regions and maturity criteria were unspecified (800–950 mm TL for females; 750 mm TL for males). In western Victoria in contrast, female L_{50} was within those length-at-maturity ranges previously reported, whereas male L_{50}'s were all lower than the respective ranges.

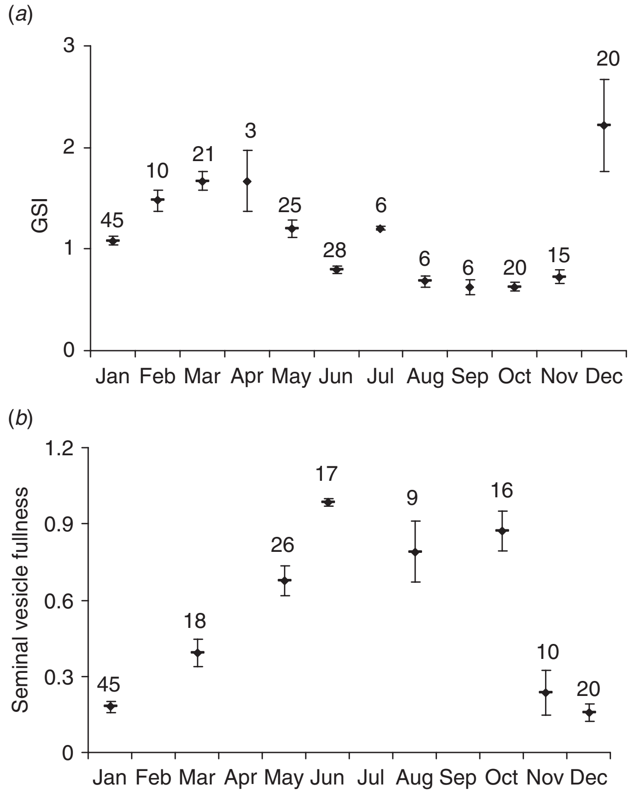

Fig. 7. Seasonality of (*a*) gonadosomatic index (GSI) and (*b*) seminal vesicle fullness for males in far-eastern Victoria. Observed mean monthly values (–), standard error bars (±1 s.e.), least-squares means corrected for effect of shark length (●), and number of observations above the bars are presented.

The differences in length–frequency distribution composition of catch samples, mass–length relationships and length-at maturity among regions and in previous studies could be the result of apparent or real differences in the population parameters. Four hypotheses are advanced; the fourth appears to best explain the differences.

(1) The differences are the result of sampling bias caused by the length-selectivity of the fishing gears. Differences in the fishing gear used to catch *Squalus megalops* from different regions have been found to cause distortions of its maturity ogives (Braccini *et al.* 2006). Although different fishing methods were used to collect *H. portusjacksoni* in the present study, specimens encompassing a wide range of sizes around the length-at-maturity were collected, making it unlikely that sampling bias would have had any marked effect on the maturity ogives.

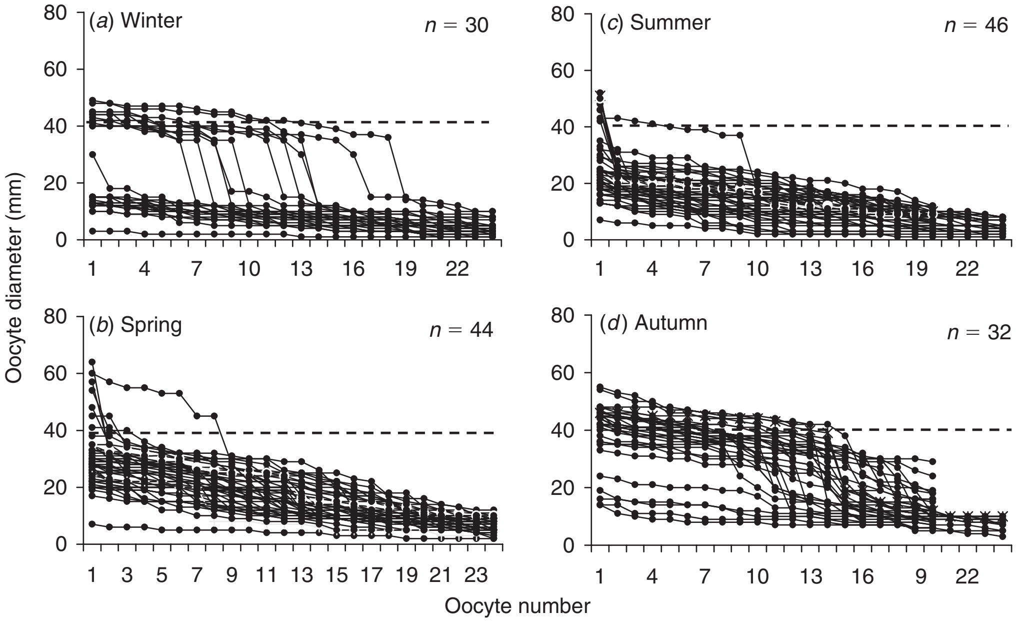

Fig. 8. Plots of the 24 largest oocyte diameters in the ovary of each mature female sampled in far-eastern Victoria. Dashed line (- - - - -) represents estimated average size of oocytes at ovulation (40 mm).

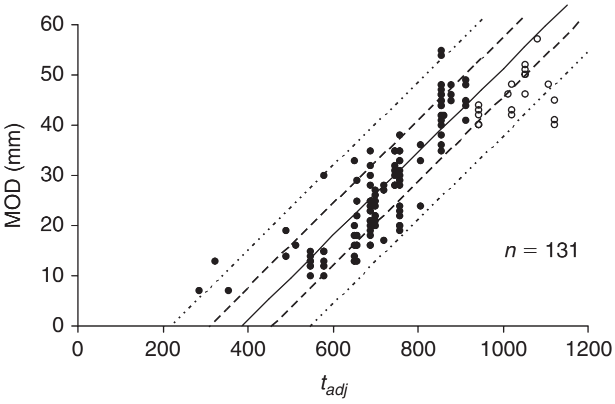

Fig. 9. Relationship between maximum oocyte diameter (MOD) and adjusted day of year (t_{adj}) (<942) for far-eastern Victoria. Linear regression (——), 95% confidence limits (– – – –) and 95% prediction intervals (- - - - -) are shown. MODs with t_{adj} >942 (○) are not used in regression analysis.

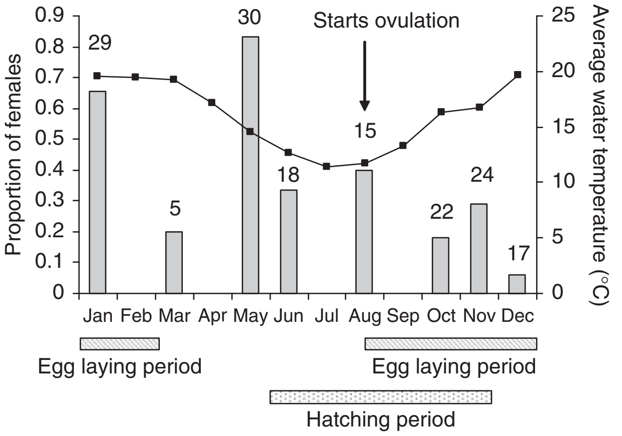

Fig. 10. Proportion of mature females with pre-ovulatory oocytes (bars) and average water temperature during each month in far-eastern Victoria. Numbers of mature females observed are presented above the bars.

(2) The differences are the result of length-selective fishing mortality caused by commercial gill-net fishing. The length-selectivity of gill-nets produced an apparent increase in length-at-maturity of *Mustelus antarcticus* populations during rising fishing mortality, with a subsequent decrease when fishing mortality declined (Walker 2007). In all the studied regions of Victoria however, the current level of fishing on *H. portusjacksoni* is low (Walker *et al.* 2005); so that the effects of length-selective fishing mortality from gill-nets is expected to be low.

(3) The differences are the result of different environmental conditions. Differences in length-at-maturity detected for other species, e.g. *Galeus eastmani*, *G. nipponensis*, *Sphyrna tiburo*, *Mustelus manazo* and *M. antarcticus*, have been related to environmental conditions such as water temperature (Horie and Tanaka 2000; Yamaguchi *et al.* 2000; Lombardi-Carlson *et al.* 2003; Walker 2007). Although western Victoria is mostly under the influence of the cold-deepwater Flinders Current and far-eastern Victoria is mostly under the influence of the warm-surface-water East Australian Current, central-eastern Victoria experiences intermediate conditions, and therefore is expected to have intermediate parameter values. However, central-eastern Victoria showed a wide range of sizes and wide confidence intervals in some estimated parameters, such as length-at-maturity, suggesting a mix of animals from western

and far-eastern populations rather than intermediate animals from a single intergrading population. Nevertheless, environmental conditions probably play a part, as these are likely to work in conjunction with genetic differences to produce differences between populations.

(4) The differences are the result of two separate breeding populations of *H. portusjacksoni* inhabiting Victorian waters, with different gene pools. This hypothesis is consistent with a conjecture, based on tagging experiments, that there are at least two separate stocks in south-eastern Australia (O'Gower and Nash 1978). One population may extend from mid NSW to central-eastern Victoria. *Heterodontus portusjacksoni* tagged near Sydney, NSW, have been recovered ~40 km south-east of Wilsons Promontory, Victoria, travelling up to 760 km (O'Gower and Nash 1978). A separate population may be present in western Victoria, with a mixing region located between Wilsons Promontory and Point Hicks.

The putative mixing region for *H. portusjacksoni* is consistent with the overlapping zone of the Peronian (Queensland 25°S, NSW and eastern Victoria) and Maugean (Victorian and Tasmanian coasts) bio-geographic provinces (Knox 1963). Overlapping zones of bio-geographic provinces depend on hydrological conditions and paleo-geographic factors involved in the evolution and distribution of species (Knox 1963, 1994). Land connection between Victoria and Tasmania, caused by changes in the sea level during glaciations, has been an important geographic and biological barrier in this region (Knox 1994), suggesting that the range of *H. portusjacksoni* has been divided and connected several times. Further studies are needed to determine the level of separation of the populations in Victoria and whether or not they interbreed in the mixing region.

Fecundity, and ovarian and reproductive cycles in far-eastern Victoria

In this region, pre-ovulatory oocytes of *H. portusjacksoni* attain a large size as compared with other species. *Galeus eastmani* and *G. nipponensis* oocytes reach a MOD of 20 and 25 mm, respectively (Horie and Tanaka 2000), whereas *Scyliorhinus retifer* reach a MOD of 18 mm (Castro *et al.* 1988). Reported MODs at ovulation for species with annual ovarian cycles are mostly <30 mm (Walker 2007). Species with MOD ~40 mm have biennial or triennial cycles, e.g. *Galeorhinus galeus* and *Squalus megalops* (Walker 2005; Braccini *et al.* 2006).

The number of pre-ovulatory oocytes is consistent with the number of eggs laid per season reported previously: 10–16 eggs (McLaughlin and O'Gower 1971), 16 eggs (Last and Stevens 1994), and 18 eggs (Gomon *et al.* 1994). These are also consistent with the number of eggs laid during a reproductive season (18) by a *H. portusjacksoni* (920 mm TL) caught in far-eastern Victoria and kept captive (Tovar-Ávila 2006). Fecundity of the species is low compared with other oviparous chondrichthyan species (e.g. *Raja brachyura*, *R. clavata*, *R. montagu*, *Scyliorhinus canicula and S. retifer*) with up to 40–150 eggs laid per year (Dodd 1983; Castro *et al.* 1988).

Difficulties in determining the seasonality of OSI and HSI in mature females could be related to the protracted ovulation and egg-laying periods, and the concurrent development of several cohorts of oocytes in the ovary. In contrast, female and male GSI and seminal vesicle fullness appear to be good indicators of the reproductive seasonality of the species in southern Australia, as found for *Mustelus antarcticus* (Walker 2007). The decrease in female GSI during spring could be related to the continuous ovulation process. The decrease in male GSI during winter–spring and the presence of semen in the seminal vesicles during winter suggest mating occurs before or during the first months of ovulation (late winter–early spring). It also suggests a need for sperm storage in the oviducal glands to ensure egg fertilisation during the long egg-laying period.

The novel method used in the present study to estimate the ovarian cycle could be useful for other species possessing seasonal reproductive cycles with oocytes at different vitellogenic stages simultaneously. The ovulation period and the egg-laying season appear to occur concurrently within individuals and with a degree of synchrony between individuals in the population. Oocytes that have reached the pre-ovulatory size before the egg-laying period are retained in the ovary until conditions are favourable for being ovulated at the end of winter–early spring. The number of pre-ovulatory oocytes then decreases during the spring and summer months because of the continuous ovulation process. Pre-ovulatory oocytes that have not reached the ovulation size by the end of winter continue growing during spring–summer, and may be ovulated if they reach ovulation size before the egg-laying period ends. Egg-laying may continue as long as water temperatures are favourable for the development of the eggs. It was observed that changes in water temperature altered the ovulation process (indicated by egg laying) in captive sharks (Tovar-Ávila 2006).

It has been stated that in oviparous species the period between first maturity (the onset of vitellogenesis) and first reproduction (the time when the animal first lays eggs) is short (Conrath 2004). However, the oocytes of *H. portusjacksoni* from far-eastern Victoria take up to 1.5 years to reach ovulation size. Furthermore, the interval between the onset of vitellogenesis and the time when free swimming animals are produced (eggs hatched) is longer. Embryonic development takes 9–12 months in this species, depending on water temperature (McLaughlin and O'Gower 1971; Rodda 2000).

Despite having a long oocyte development period, the presence of several oocyte cohorts in the ovary suggests that *H. portusjacksoni* has an annual reproductive cycle. However, the presence of some mature females lacking pre-ovulatory oocytes during the months previous to the reproductive season suggests that there may be a seasonal resting period for a proportion of the female population, as reported for other shark species, such as *Carcharhinus acronotus* (Hazim *et al.* 2002).

The presence of *corpora lutea* and *corpora atretica* may be good indicators of completion of ovulation (Bragdon, in Hisaw and Hisaw 1959). Although oocyte atresia can occur at any stage of oocyte growth (Hisaw and Hisaw 1959), the increase in the number of *corpora atretica* following the egg-laying period in *H. portusjacksoni* appears to be related to the end of ovulation and the absorption of large non-ovulated oocytes.

We have presented a novel approach to determine the ovarian cycle of an oviparous chondrichthyan species, which may be useful for other such species. The regional differences found in some reproductive and morphometric parameters of

H. portusjacksoni provide evidence of two populations off Victoria, but other methods, such as genetic techniques and tagging studies in Victorian waters, are needed to confirm this. If the populations are distinct, the reproductive parameters need to be determined separately for western Victoria for population modelling purposes. This paper provides those parameters for the population in far-eastern Victoria.

Acknowledgements

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Dorsal-fin spine growth of *Heterodontus portusjacksoni:* A general model that applies to dorsal-fin spines of chondrichthyans?

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Abstract: A prospective model of dorsal-fin spine growth in chondrichthyans is devised by studying the growth of spines from captive and wild *Heterodontus portusjacksoni* injected with several fluorochromes. Evidence was found for only two dentine layers in the spine trunk of *H. portusjacksoni*, contrasting with conjectures about the presence of a third middle dentine layer in some squalids. The spines have three simultaneous growth zones. The first growth zone is along the internal edge of the inner trunk dentine layer, where growth bands are deposited towards the centre (centripetally) increasing spine length and width by pressure against the cartilage rod. The second growth zone is along the external edge of the outer trunk dentine layer at the spine base, where growth bands are deposited in opposite direction to the centre (centrifugally) increasing spine width. A third growth zone at the base of the cap enables downwards expansion over the trunk. The model of "concentric cones" describes correctly the inner dentine layer growth pattern, whereas the outer dentine layer growth-increments appear to be related to the external bands on the surface of the trunk. Growth-increments from the three growth zones of the spine are all potentially useful for age estimation.

Keywords: Port Jackson shark, sharks, holocephalans, calcified structures, ageing.

Introduction

Chondrichthyan age estimation is mostly achieved by counting the number of growth-increment bands in hard-tissue structures such as calcified vertebrae and dorsal-fin spines. The presence of dorsal-fin spines in some groups of sharks, as well as in holocephalans, is potentially useful for age estimation, but a lack of understanding of the internal structure and growth patterns of dorsal-fin spines has limited their use. Dorsal-fin spines are used for ageing some squalid sharks and holocephalans (Cailliet and Goldman 2004), but their use is not reported for heterodontid sharks.

The indented structure of dorsal-fin spines of chondrichthyans has been described, and its morphogenesis in heterodontid and squalid sharks is similar (Maisey 1979). The spine consists of a cap covering the upper region of the spine, the spine trunk, and an inner pulp cavity above a cartilaginous rod (Fig. 1). The cap comprises an external enamel layer and other associated tissues, such as the mantle. Often confused with the entire cap, the mantle is only a thin dentine layer penetrated by longitudinal vascular canals called mantle canals. The trunk is formed by concentric layers of dentine, each separated by a trunk primordium. The trunk dentine layers (TDLs) are distinct from the dentine layer of the mantle and separated from this by the transitional layer. Odontoblasts on those parts of the external surface of the outer TDL not covered by the cap are involved in the dentine formation (dentinogenesis) of the outer TDL (Maisey 1979).

Insert
Fig 1

Ridges on the external surface of the spine cap (enamel bands) are widely used for ageing *Squalus acanthias* and *S. megalops* (Holden and Meadows 1962; Beamish and McFarlane 1985; Braccini et al. 2007), but cross-sections of spines are used for species where a banding pattern on the cap surface is not evident or distinguishable (Tanaka

1990; Clarke et al. 2002a; Calis et al. 2005). More recently ridges on the surface of the spine trunk, referred as "external bands", were used to age *Centroselachus crepidater* (Irvine et al. 2006). These authors agree that the spine trunk is formed by TDLs, but the number of layers and the way they are deposited remain uncertain. Some authors recognize the presence of two TDLs (Maisey 1979; Clarke et al. 2002a; Calis et al. 2005), whereas others report a third middle TDL (Beamish and McFarlane 1985; Tanaka 1990; Irvine et al. 2006).

Incorporation of oxytetracycline (OTC) on the spine cap surface, the base of the spine and the inner TDL of spines of *Squalus acanthias* suggests an annual growth-increment banding (Beamish and McFarlane 1985). There is no published evidence, however, that the middle and inner TDLs are separated. As pointed out by Clarke et al. (2002a), the presence of discontinuities in the inner TDL may have led some authors to interpret part of this layer as a middle TDL. Determining the number of TDLs is essential because of the possibility of under- or over-estimation of age, with potential flow-on effects of biased fishery assessment and misguided management (Summerfelt and Hall 1987; Campana 2001).

To better understand the growth pattern of the dorsal-fin spines of the Port Jackson shark (*Heterodontus portusjacksoni*) and other chondrichthyans, we examined the structure and growth of the spines from captive and wild *H. portusjacksoni* injected with several fluorochromes as hard tissue dyes. Endemic to southern Australia (Last and Stevens 1994), *H. portusjacksoni* is commonly caught as bycatch by several commercial fisheries (Walker et al. 2005). Age information for this species is required to better understand its population dynamics and the effects of fishing on its populations, so that understanding the growth pattern of dorsal-fin spines is of critical importance.

Materials and methods

Use of fluorochromes in captive sharks

Five female *H. portusjacksoni* were held captive for 1.5−2.0 years. These specimens were obtained from the commercial catches in Mallacoota, Victoria, and transported in a 1000-L tank with seawater and constant air supply to the laboratories of Primary Industries Research Victoria in Queenscliff, Victoria. During the first 18 months of the study, they were kept in an outdoor 27 000-L circular tank (~7 m diameter and ~1.5 m deep) with a constant flow of seawater pumped from Port Phillip Bay, Victoria (10 000 $L \bullet h^{-1}$). The temperature of the water in the tank varied seasonally with ambient water temperature in the Bay; average daily water temperatures varied from 11.4°C during winter to 19.7°C during summer. The sharks were exposed to normal day and night and normal seasonal light variation. A shade-cloth roof was placed over the tank to reduce sunlight intensity. During the last 9 months of the study, the sharks were transferred to a smaller indoor 5000-L circular tank. Water conditions were similar to those for the earlier part of the study, but artificial light was used to illuminate the tank during daylight hours. The sharks were fed to satiation three times a week, mainly with pilchards. They were occasionally fed live sea urchins, squid, clams, mussels and prawns.

The sharks were measured, weighed and injected with fluorochromes every 6 or 12 months, a single fluorochrome being injected at a time. Total length (TL) was measured to the nearest mm as a straight line from the tip of the snout to the distal end of the tail, while the shark was in a natural position without stretching it. Mass was recorded with a spring balance ± 25 g. Three different fluorochrome hard-tissue dyes─oxytetracycline (OTC) (Terramycin/LA, Pfizer), alizarin red S (ARS) (Aldrich), and calcein (Sigma-Aldrich)─were used to provide a "date stamp" against which to compare the position of growth-increment bands formed subsequently. These fluorochromes were successfully used in other shark ageing studies, and produced fluorescent marks in vertebrae (Officer et al. 1997) and spines (Beamish and McFarlane 1985), persisting as marker of growth for extensive periods of time (Smith et al. 2003). All fluorochromes were used at a concentration of 25 $mg \cdot kg^{-1}$ shark mass, based in experiments on the toxicity of OTC in *H. portusjacksoni* (Walker et al. 1995) and other species (Officer et al. 1997), and on the incorporation time of this fluorochrome in the species (Izzo et al. 2007). Fluorochrome (OTC) marks are visible in sections of the dorsal fin spines of *H. portusjacksoni* 2-days after treatment, thus there is no significant time-lag between fluorochrome injection and band formation (Izzo et al. 2007).

Use of fluorochromes in wild sharks

The spines of eight sharks (five males and three females) injected with OTC and released into the wild were analysed after recapture. These sharks were at liberty for periods between 149 and 314 days. All injected wild sharks were caught and tagged during commercial trawling operations and during surveys on board RV *Ngerin* between April 2004 and March 2005 in Spencer Gulf, South Australia. Wild sharks were measured in the same way as captive sharks, weighed and tagged with rototags (Dalton ID Systems LTD, Oxon, U.K.). Doses of OTC used for these sharks were similar to those used for captive animals. Tagged specimens were allowed to recover on board in seawater tanks for 30–45 min prior to being released.

Tissue collection and processing

Sharks were sacrificed with an overdose of the anaesthetic benzocaine. After sacrifice of the animals, both first and second dorsal-fin spines from all injected sharks (captive and wild) were removed by cutting the spines at their base over the vertebral column. Spines were cleaned with a scalpel and washed with tap water. After cleaning, the spines were air-dried and stored in labelled paper envelopes in a dark cool place to avoid loss of fluorescence. Longitudinal and cross-sections of the spines (~300 μm thick) were cut using a lapidary saw (Gemmasta®) after embedding the structures in polyester resin. Cross-sections were taken every 2 mm from the tip to the base of the spine. The sections were mounted on glass microscope slides and sealed with cover slips.

Interpretation of growth-increment bands

The dorsal-fin spine terminology used follows Maisey (1979) as this proved to be consistent with the spines external and internal structure, whereas the age and growth related terms used follow in general Clarke and Irvine (2006).

The sections were examined and photographed under a compound microscope using ultra-violet (UV) light with an attached camera (Leica DC300F) and a variety of filter blocks appropriate to the fluorochromes used (Officer 1995) (Table 1). The number of growth-increment bands (enamel bands, external bands and growth-increment bands in the TDLs), discontinuities, and presence and positions of the fluorescent marks in each part of the spines were recorded. A growth-increment band consists of an opaque zone and a translucent zone in the spine TDLs (Cailliet and Goldman 2004) when viewed unstained with transmitted light. Enamel bands comprise ridges on the surface of the spine caps, whereas external bands comprise growth-increment bands on the surface of the trunk (Clarke and Irvine 2006). A discontinuity consists of an abrupt check or band within a TDL traversed by blood vessels (canaliculi) (Clarke et al. 2002a). False fluorescent marks produced by autofluorescence of some proteins in the tissues surrounding the structures were distinguished by their colour (OTC appears gold or yellow, whereas autofluorescence appears green or blue under certain UV wavelengths) and by close inspection of the marks at 10× or 25× magnification (Fielder 2002). An ordinal scale of the intensity of the fluorochromes adapted from Logsdon et al. (2004) was used (Table 2). Records were made of whether the fluorescent mark was part of a translucent band or an opaque band, and the number of growth-increment bands formed after or between the fluorescent marks was counted and compared with the time-at-liberty or time-in-captivity to determine if these bands are formed annually. Three non-consecutive growth-increment band counts were made for each section, without prior knowledge of the animal's length, sex or previous counts. The first translucent band was interpreted as the first winter (birth band), as the eggs of the species commonly hatch during winter; the subsequent translucent bands were interpreted as completed years of age.

Insert tables 1 and 2

Comparisons of the number of growth-increment bands and the presence or absence of florescent marks between sex or size groups were not undertaken because of the limited number of specimens for each sex and size. Instead, a general model was developed assuming a similar growth pattern of the dorsal-fin spine in both sexes.

Results

All captive and wild sharks grew in length and mass during the study with the exception of two individuals. A captive shark decreased in mass during the last few months of the experiment, and a wild shark that was shorter at recapture than at release (Table 3). The lengths of sharks analysed range from 377 to 970 mm TL and the apparent ages from 1 to 18 years for females; and from 430 to 660 mm TL and from 3 to 12 years for males.

Insert table 3

The three injected fluorochromes (OTC, ARS and calcein) were observed under UV light in the dorsal-fin spines of all the captive and wild sharks. The fluorescent marks appeared as a discrete line near the base of the spine cap (Fig. 2) (intensity scores over 2 for all fluorochromes). Evidence of only two TDLs, separated by a conspicuous primordium, was found in the spine trunk. A fluorescent marks appeared as rings near the internal edge of the inner TDL (close to the pulp cavity) (intensity scores over 2 for all fluorochromes), and near the external edge of the outer TDL in cross-sections of spines (intensity scores 1−2 for all fluorochromes), but only in sections below the skin and close to the base of the spine (Fig. 3, 4 and 5). Fluorescent marks appeared also as a ring near the internal edge of the mantle canals (Fig. 5b) (intensity scores 1−2 for all fluorochromes).

Insert figures 2-5

Fluorescent marks in cross-sections of the spine showed that the inner TDL grew centripetally towards the pulp cavity (Fig. 3), whereas the fluorescent marks in longitudinal sections showed that these growth-increment bands were deposited along the entire length of the spine where the pulp cavity is open (Fig. 4). In these sections, individual growth increments in the outer TDL could be followed only along some regions of the spine, ending before reaching the tip of the spine or the base of the spine. The upper limit of these outer TDL layers was observed to reach the outer edge of the spine trunk, although the outer TDL layer edges were often not clear. Fluorescent marks were also found around the outer TDL in longitudinal and cross-sections only in the region below the skin, close to the base of the spine (Figs. 4 and 5). Fluorescence appeared irregular and patchy along the edge of outer TDL in longitudinal sections, being most distinct at the very base of the spine.

A prominent discontinuity in the inner TDL was observed in some spine sections, but no fluorescent marks were observed around it (intensity score 0 for all fluorochromes), indicating this is not a growth area. Prominent discontinuities were found in sections of dorsal-fin spines of sharks larger than 900 mm TL (Samples E4972 and C1998) (Fig. 3a), but were absent in smaller specimens. The inner TDL canaliculi originate in the peripheral tissues of the pulp cavity, always crossing all the inner TDL (including the discontinuity if present) to reach the trunk primordium. The outer TDL canaliculi originate at the transitional layer in the region where the cap is present, or at the odontoblast layer below the insertion of the skin, crossing to the trunk primordium in the opposite direction to the inner TDL canaliculi.

Fluorescent marks from fluorochromes injected during winter months were found in the translucent bands, whereas fluorescent marks from fluorochromes injected during summer months were found in the opaque bands.

Discussion

The fluorescent marks found in sectioned spines of *H. portusjacksoni* in this study, at the base of spine caps, in the inner TDL and in some parts of the outer TDL, indicate that these structures have three growth zones. The first growth zone is along the internal edge of the inner TDL where growth bands are deposited towards the centre of the pulp cavity (centripetally), increasing spine width and length by pushing against the cartilage rod (Fig. 6). The second growth zone is at the spine trunk periphery, along the external edge of the outer TDL at the base of the spine, where growth bands are deposited in the opposite direction to the centre (centrifugally) resulting in the formation of the external bands. The third growth zone is at the base of the cap producing a downward extension of the cap to continuously cover the spine trunk as it grows outwards from the skin. Evidence of fluorescence on spine caps, in the inner TDL and on the surface of the base of the spine trunk of *Squalus acanthias* (Beamish and McFarlane 1985) suggests that this growth pattern could be similar in the dorsal-fin spines of other chondrichthyan species.

Insert figure 6

The inner TDL growth pattern is such that new growth-increment bands are not formed in the more distal region of the spine where the pulp cavity has been completely filled. This interpretation is supported by the lack of fluorescent marks in cross-sections of the distal region of the spine and by lower counts of growth-increment bands in cross-sections of the distal region than counts in cross-sections through regions of the spine where the pulp cavity is open (Tovar-Ávila 2006). Because of continuous growth in length and width of the spine at its base, the pulp cavity is never completely filled by the inner TDL growth-increments.

The fluorescent marks showed that the outer TDL grows only below the skin and mostly in the region close to the base of the spine where the odontoblasts are present (Maisey 1979). Consequently, cross-sections at any level of the spine are unlikely to show all the outer TDL growth-increment bands. Sections close to the base of the spine may show the newest growth-increment bands in the outer TDL, whereas sections above the skin will show progressively earlier growth-increment bands farther up the spine trunk. This is consistent with the number of growth-increment bands in the outer TDL from any section along the spine being less than the number in the inner TDL (Tovar-Ávila 2006). Clear sections at the very base of the spine were difficult to obtain due to the trunk in this region being thinner because it consists only of the new outer TDL growth-increment bands and it loses its form when cleaned and dried.

Our fluorescence results are consistent with the hypothesis that there are two TDLs in the spines of *H. portusjacksoni*, as proposed for some chondrichthyan species (Maisey 1979; Clarke et al. 2002a; Calis et al. 2005) rather than three TDLs as proposed for other chondrichthyans (Beamish and McFarlane 1985; Tanaka 1990; Irvine et al. 2006). The available evidence of growth regions based on injected specimens of *Squalus acanthias* (Beamish & McFarlane 1985) and *H. portusjacksoni* (present study) with OTC supports the interpretation that the appearance of a middle TDL is related to discontinuities in the inner TDL (Clarke et al. 2002a). The variable prominence of the discontinuity and its absence in some young specimens indicate that the discontinuity could be related to severe alterations in growth pattern through the life of the shark. Discontinuities in other calcified structures of fish such as otoliths are frequent and are attributed to alterations in growth pattern (e.g. adverse conditions or reproductive periods) and several types of discontinuities can be observed, from small gaps to major unconformities that can be traced continuously along the entire calcified structure (Morales-Nin 1987).

If the separation between the inner and middle TDLs is only a major unconformity, studies considering the inner TDL as two separated layers for growth-increment band counts would under-estimate shark age. Under-estimation (rather than over-estimation) of age inevitably produces demographic parameters that lead to overly optimistic prognoses in fishery stock assessment (Summerfelt and Hall 1987; Campana 2001).

Results from the present study are consistent with the "concentric-cones" growth model of the spine proposed by Holden and Meadows (1962) for the growth of the inner TDL, but not for growth of the whole spine. Consistent with the results of Beamish and McFarlane (1985), our results do not support the Holden and Meadows conjecture that the inner TDL annuli (the cone bases) correspond to the annuli on the surface of the cap; but nor do they correspond to the external bands as proposed by Beamish and McFarlane. Similar growth-increment band counts between the surface of trunk, the surface of the spine cap and the inner TDL led Holden and Meadows to their interpretation, but Beamish and McFarlane (1985) provided evidence that the spine cap forms independently of the trunk. Beamish and McFarlane (1985) then assumed that the inner TDL annuli correspond to the external bands at the base of the spine as a result of discontinuous growth lengthening the spine. However, fluorescent marks in longitudinal and cross-sections from our study show that the inner TDL grows along the entire length of the spine adjacent to the pulp cavity, which is consistent with the "concentric-cones" growth model for the inner TDL, but never reaches the surface of the base of the spines to form the external bands because the outer TDL always surrounds the inner TDL.

The explanation of Beamish and McFarlane (1985) for the formation of growth-increment bands in the trunk appears to be correct only for the outer TDL, as they consist of layers deposited by the odontoblasts surrounding the trunk (Maisey 1979) at the base of the spine, growing in a differential way as the trunk moves away from the base.

Therefore, each external band observed in the surface of the trunk corresponds to the upper limit of an outer TDL growth-increment band. These external bands become smaller and closer together as the shark growth diminishes in adults. In the present study the external bands on the surface of the trunk were observed only on the part of the spine below the skin, because of difficulty in separating the cap from the trunk. A similar problem was found in *S. acanthias* (Beamish and McFarlane 1985).

The formation of enamel bands has been explained by an asynchronous growth of the cap and the spine trunk, where during periods of slow upward growth of the trunk the cap downward growth is not reduced (Beamish and McFarlane 1985), but this is inconsistent with both the cap and the spine trunk being subjected to the same mechanisms affecting growth. Instead, enamel bands may well be related to a hypermineralization or accumulative process during periods of slow growth similar to that occurring in the growth-increment bands of vertebrae of teleosts (Morales-Nin 1987) and some chondrichthyans species such as *Mustelus antarcticus* (Officer et al. 1997). Beamish and McFarlane (1985) noted that the highest concentration of pigment and thickening of the enamel correspond to periods when the spine growth is reduced. Further studies on the hypermineralization of bands in chondrichthyan dorsal-fin spines are needed to clarify if the process is similar to other calcified structures.

The use of enamel bands of *Squalus acanthias* is suggested as the most convenient method to age this species, because the inner TDL annuli are less prominent (Beamish and McFarlane 1985). This is not the case for *H. portusjacksoni*, where growth-increments in both spine growth zones are distinguishable. Furthermore, some deepwater dogfishes have a reduced spine cap with unclear annuli, which makes spine sectioning or the use of external bands the most suitable ageing methods (Clarke et al. 2002a, 2002b, Irvine et al. 2006). Large *S. acanthias* may have also a worn spine surface with no remaining pigment in distal portions of the spine cap (Holden and Meadows 1962; Ketchen 1975) so that the early enamel bands would be missed and alternative methods would be needed.

The positions of the fluorescent marks suggest that enamel bands form annually in the cap, whereas pairs of alternating opaque and translucent growth-increment bands formed annually in the TDLs of the spine. The spines of *H. portusjacksoni* appear to deposit a translucent growth-increment band in winter and an opaque band in summer, which is similar to the growth pattern observed in other chondrichthyan structures (Sullivan 1977; Cailliet and Goldman 2004). Full validation of ageing of *H. portusjacksoni* will require the analysis of growth-increment band formation in all age groups (Campana 2001).

In conclusion, dorsal-fin spines of *H. portusjacksoni* have three zones of simultaneous dentinogenesis causing its growth in different directions, and only two dentine layers in their trunk. Growth-increment bands from all the three growth zones—enamel bands, external bands resulting from the outer TDL growth-increment bands, and growth-increment bands in the inner TDL—are potentially useful for age estimation because all of them are affected by the same endogenous and exogenous mechanisms involved in shark growth. Analogous morphology of dorsal-fin spines between heterodontid and squalid sharks (Maisey 1979), as well as some similarities with holocephalans (Calis et al. 2005), suggest that this model of growth devised for *H.*

portusjacksoni could be applicable to all chondrichthyans possessing dorsal-fin spines. However, future research in other chondrichthyan groups is required to test the model.

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Table 1. Excitation and emission wavelengths of the dichroic mirror filters used for the examination of the fluorochomes used. OTC, oxytetracycline, ARS, alizarin red stain. Filter block code by Leica Instruments P/L, Victoria, Australia.

Fluorochrome	Filter block code	Excitation range (nm)	Emission range (nm)
OTC	D	355–425	>460
Calcein	I3	450–490	>520
ARS	N2.1	515–560	>580

Table 2. Ordinal scale of the intensity of oxytetracycline marks in calcified structures of elasmobranches (adapted from Logsdon *et al.* 2004).

Score	Intensity	Definition
0	Absent	No mark present
1	Faint	The mark is present but not clearly visible
2	Visible	The mark is readily visible but not vivid
3	Intense	The mark is both readily visible and vivid

Table 3. Fluorescent marker injections in captive and wild sharks. OTC, oxytetracycline, ARS, alizarin red stain.

Sample number	Sex	Capture		Date of injection			Period of survival (months)	Sampling		
		Length (mm)	Mass (g)	OTC	ARS	Calcein		Date	Length (mm)	Mass (g)
Captive sharks										
E4972	F	906	7100	25/07/2003	13/07/2004	14/12/2004	18	10/01/2005	920	7600
E4971	F	855	5950	25/07/2003	13/07/2004	14/12/2004	24	15/08/2005	880	6850
E4970	F	865	5500	19/12/2003	14/12/2004		15	09/08/2005	875	6500
E4973	F	795	5100	19/12/2003	14/12/2004		20	15/08/2005	805	6800
C1998	F	960	8400	13/07/2004		14/12/2004	14	07/10/2005	970	8150
Wild sharks										
PJ622	F	393		11/11/2004			5	09/04/2005	377	
PJ45	F	394		09/09/2004			11.1	09/08/2005	445	
PJ788	F	771		13/11/2004			6.8	04/06/2005	790	
PJ810	M	401		22/01/2005			5.3	01/07/2005	430	
PJ826	M	445		21/01/2005			5.4	03/07/2005	475	
PJ933	M	519		21/01/2005			5.5	05/07/2005	539	
PJ597	M	557		13/11/2004			6	13/05/2005	574	
PJ768	M	647		13/11/2004			6.1	14/05/2005	660	

Figure captions

Fig. 1. Diagram of a dorsal-fin spine from *Heterodontus portusjacksoni* (modified from Maisey 1979). (a) Longitudinal section and (b) cross-section at the level of the arrow. PC, pulp cavity; TDL, trunk dentine layer; TP, trunk primordium; TL, transitional layer; MC, mantle canals. Uncertain cartilage rod and pulp cavity height relative to the TDLs.

Fig. 2. Enamel band formation on the cap of the whole first dorsal-fin spine (female E4971, 855 mm TL, sacrificed August 2005) viewed under UV light with OTC (a) and calcein (b) filters. Scale bar= 0.5 mm.

Fig. 3. Cross-section of a dorsal-fin spine of a shark injected with OTC, alizarin red stain, and calcein, viewed under white light (a) and UV light using different filters (b, c and d), to show growth-increment band formation in the inner trunk dentine layer (female E4972, 906 mm TL, sacrificed January 2005). Remains of tissues in the pulp cavity show autofluorescence. Scale bar= 0.5 mm.

Fig. 4. Longitudinal sections showing the inner trunk dentine layer (ITDL) and outer trunk dentine layer (OTDL) at the middle level of the spine viewed under white light (a), and under UV light for same section (b) to show the OTC mark in the ITDL (female E4970, 865 mm TL, sacrificed August 2005). ITDL and OTDL at the base level of the spine viewed under white light (c), and under UV light for the same section (d) to show the OTC mark in both TDLs (female E4971, 855 mm TL, sacrificed August 2005). Autofluorescence can be seen in the edge of both TDLs in (b). Scale bars= 0.5 mm.

Fig. 5. Cross-section from a dorsal-fin spine viewed under white light (a) and same section under UV light (b), showing the OTC mark in the inner trunk dentine layer

(ITDL), outer trunk dentine layer (OTDL) and mantle canals (MC), at the level of spine insertion in the skin (male PJ597, 574 mm TL, 181 days at liberty). Cross-sections viewed under UV light (c and d), showing the OTC mark in the ITDL and OTDL at the level of the base of the spine (c), and magnification of the inner rectangle (d) (male PJ810, 430 mm TL, 160 days at liberty). TP, trunk primordium; PC, pulp cavity; C, cap. Autofluorescence can be seen in the edge of both TDLs. Scale bars= 0.5 mm.

Fig. 6. Diagrammatic representation of the growth of a 5-year-old spine (considering the first growth increment or enamel band as the birth mark), based on Holden and Meadows (1962) "concentric-cones" model for the inner trunk dentine layer. Thin solid lines represent growth-increment bands for the inner trunk dentine layer and dotted lines for the outer trunk dentine layer. Thick arrows show the regions and direction of growth of the trunk layers. Cap is not shown. Uncertain cartilage rod height relative to the inner trunk dentine layer.

Table 1. Fluorescent marker injections in captive sharks.

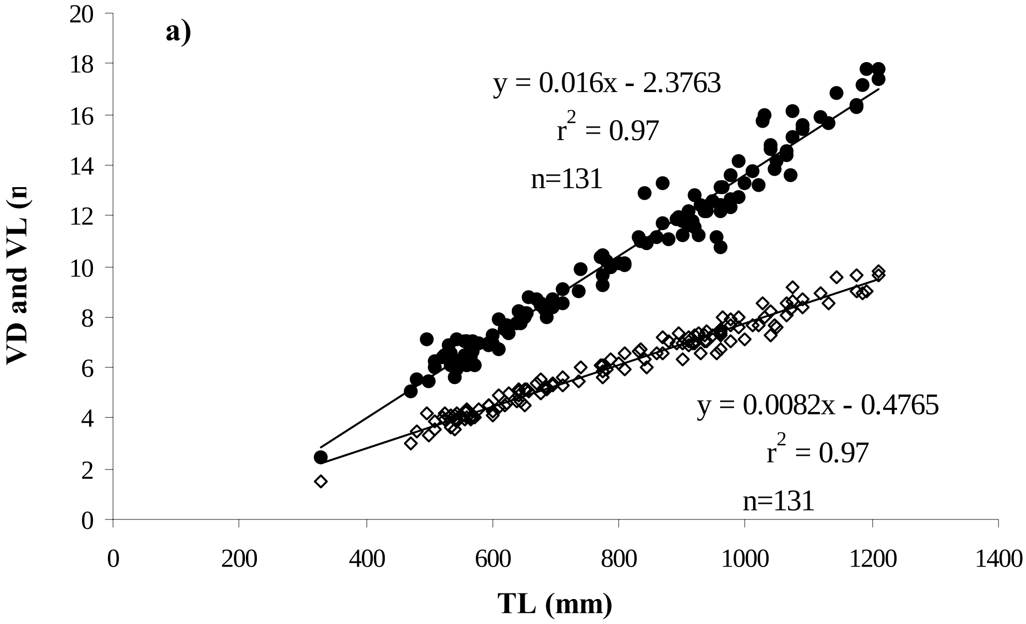
Sample Number	Length at 1st injection (mm)	2003		2004		Time alive after 1st injection (months)	Sampling date	Length at sampling (mm)
		Winter (25/Jul)	Summer (19/Dec)	Winter (13/Jul)	Summer (14/Dec)			
E4972	906	OTC		Alizarin red	Calcein	18	10/Jan/05	920
E4971	855	OTC		Alizarin red	Calcein	24	15/Aug/05	
E4970	865		OTC		Alizarin red	15	9/Mar/05	
E4973	795		OTC		Alizarin red	20	15/Aug/05	
C1998	960			OTC	Calcein	14	7/Oct/05	970

OTC= Oxytetracycline

Table 2. Reader confidence and precision indices for each structure and method.

	Vertebrae		Spines				
	Whole	Sectioned	Whole (combined)	1st whole	2nd whole	Sectioned (Inner trunk)	Sectioned (Outer trunk)
Reader confidence		3.3[1]	3.5[1]	3.5[1]	3.6[1]		
	(2.16[2])	(2.1[2])	(2.63[2])	(2.8[2])	(2.83[2])	(2.28[2])	(2.18[2])
IAPE		8.9	10.1	9.3	11.2		
	(8.66)	(10.6)	(10.3)	(11.2)	(9.58)	(7.05)	(7.08)
CV		10.9	13.4	12.5	14.4		
	(12.2)	(13.5)	(14.49)	(15.8)	(13.6)	(9.97)	(10.02)

(Javier´s indices) [1] Green´s *et al.* readability score [2] Officer´s *et al.* readability score



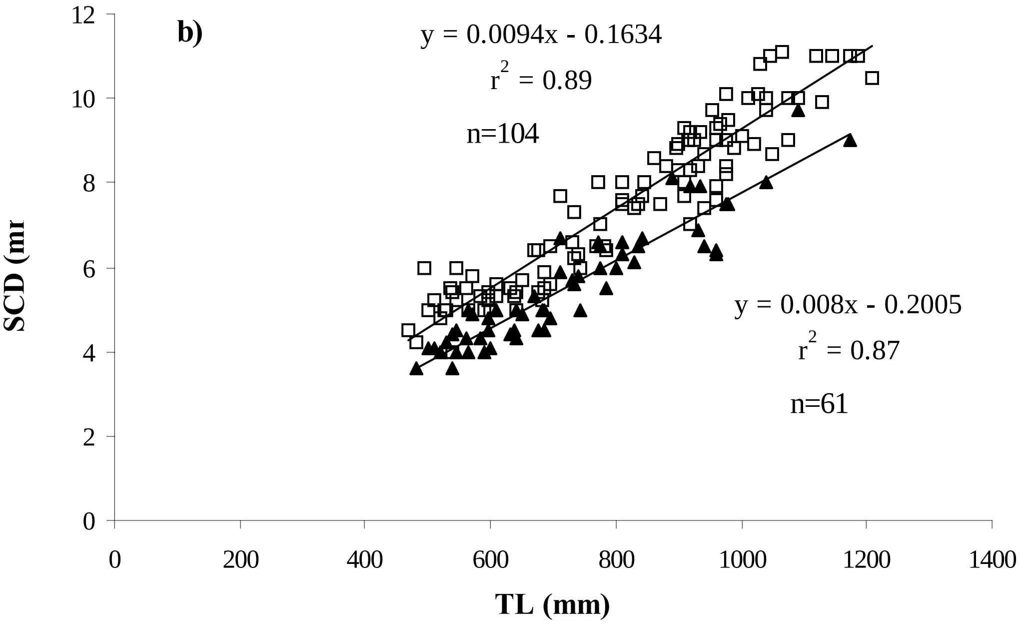
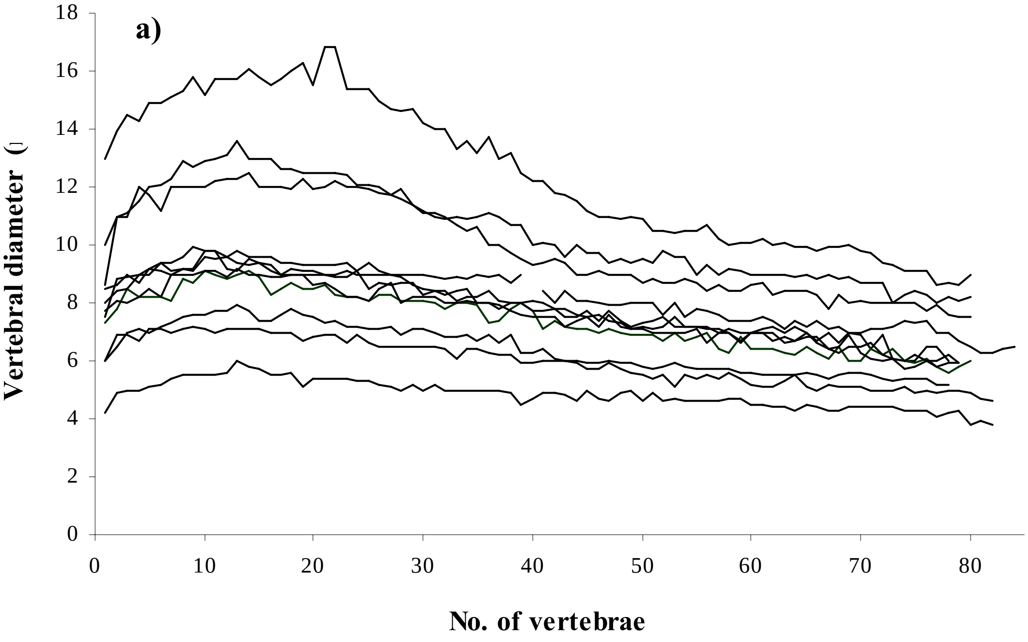


Figure 2. Total length (TL) versus vertebral diameter (VD•) and vertebral length (VL◊) (a), and versus spine cap diameter (SCD) for the first spine (□) and second spine (▲) (b) in the Port Jackson shark



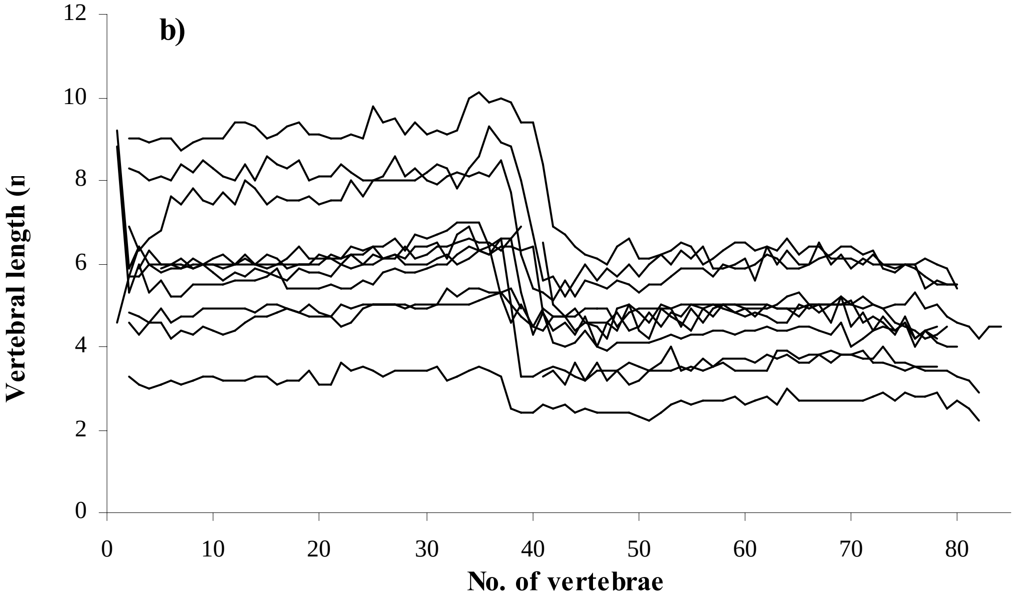
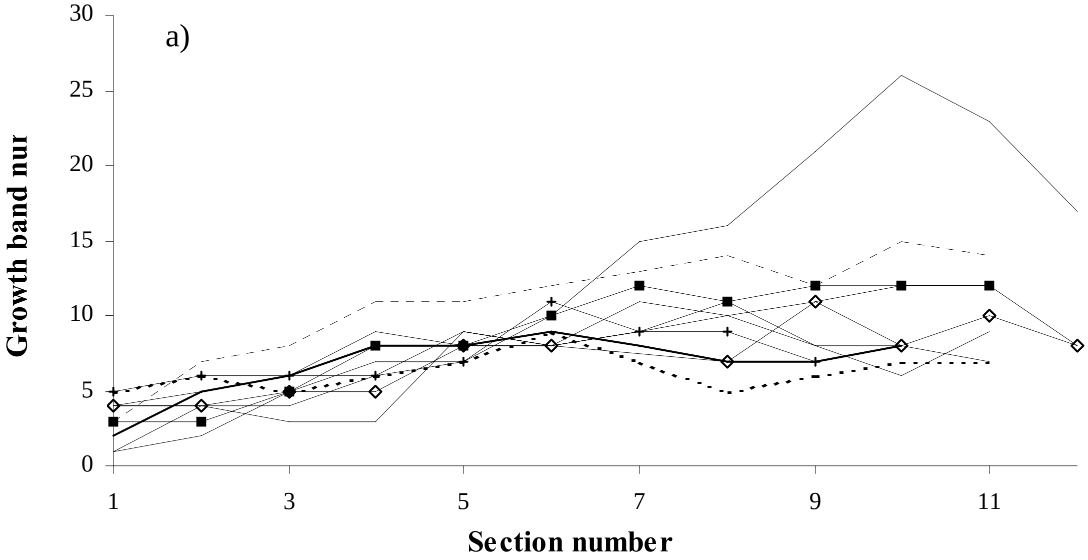


Figure 3. Variation on the vertebral diameter (a) and length (b) along the vertebral column in ten Port Jackson sharks.



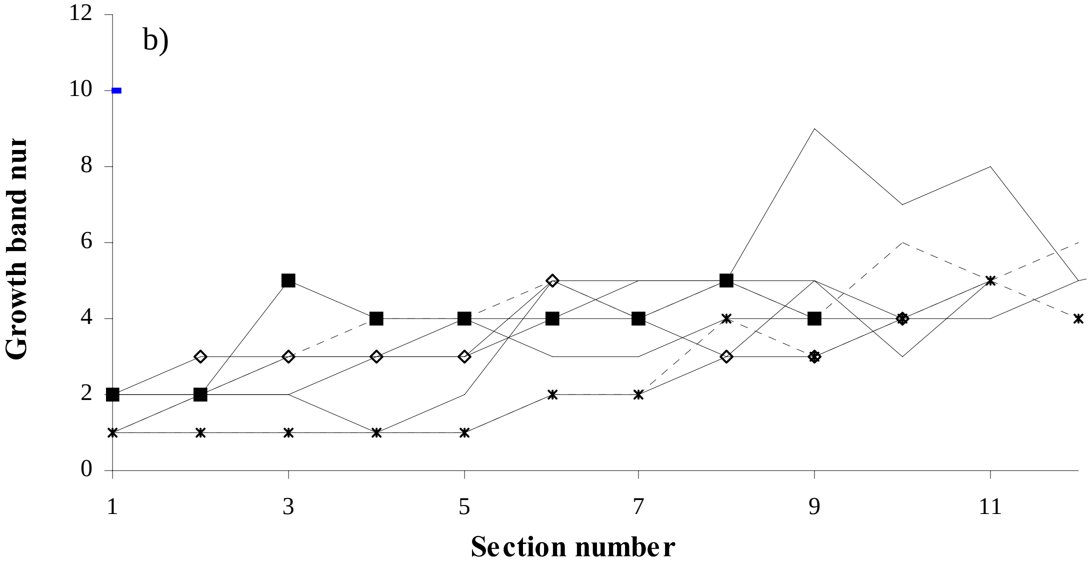


Figure 9. Variation in the number of growth bands in the inner trunk layer (a) and outer trunk layer (b) from sections along the dorsal spine of ten Port Jackson shark.

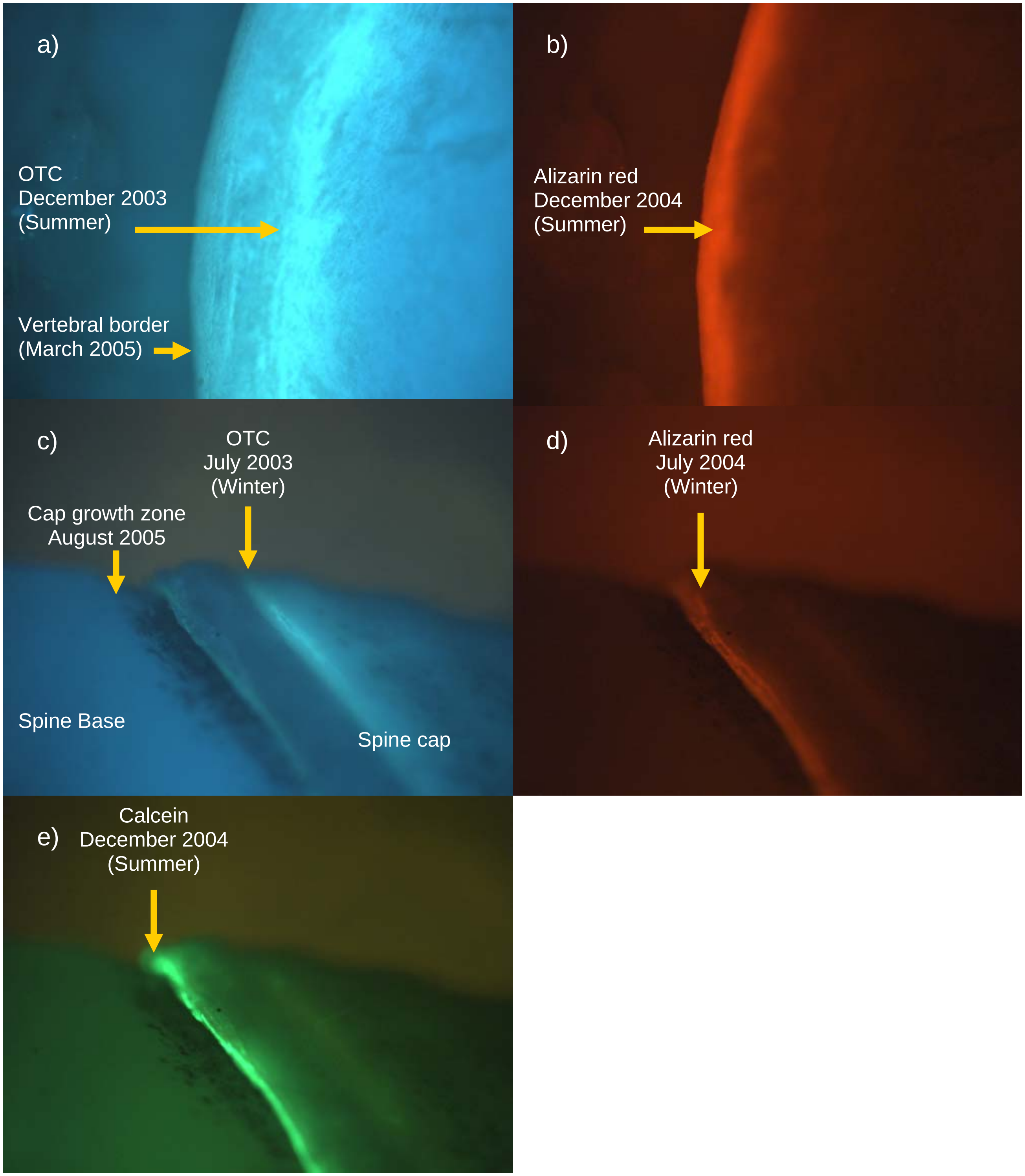


Figure 4. Growth band formation in a whole vertebrae (a and b) from a female of 865 mm TL (E4970), sacrificed in March 2005; and the whole first dorsal spine (c, d and e) from a female of 855 mm TL (E4971), sacrificed in August 2005.

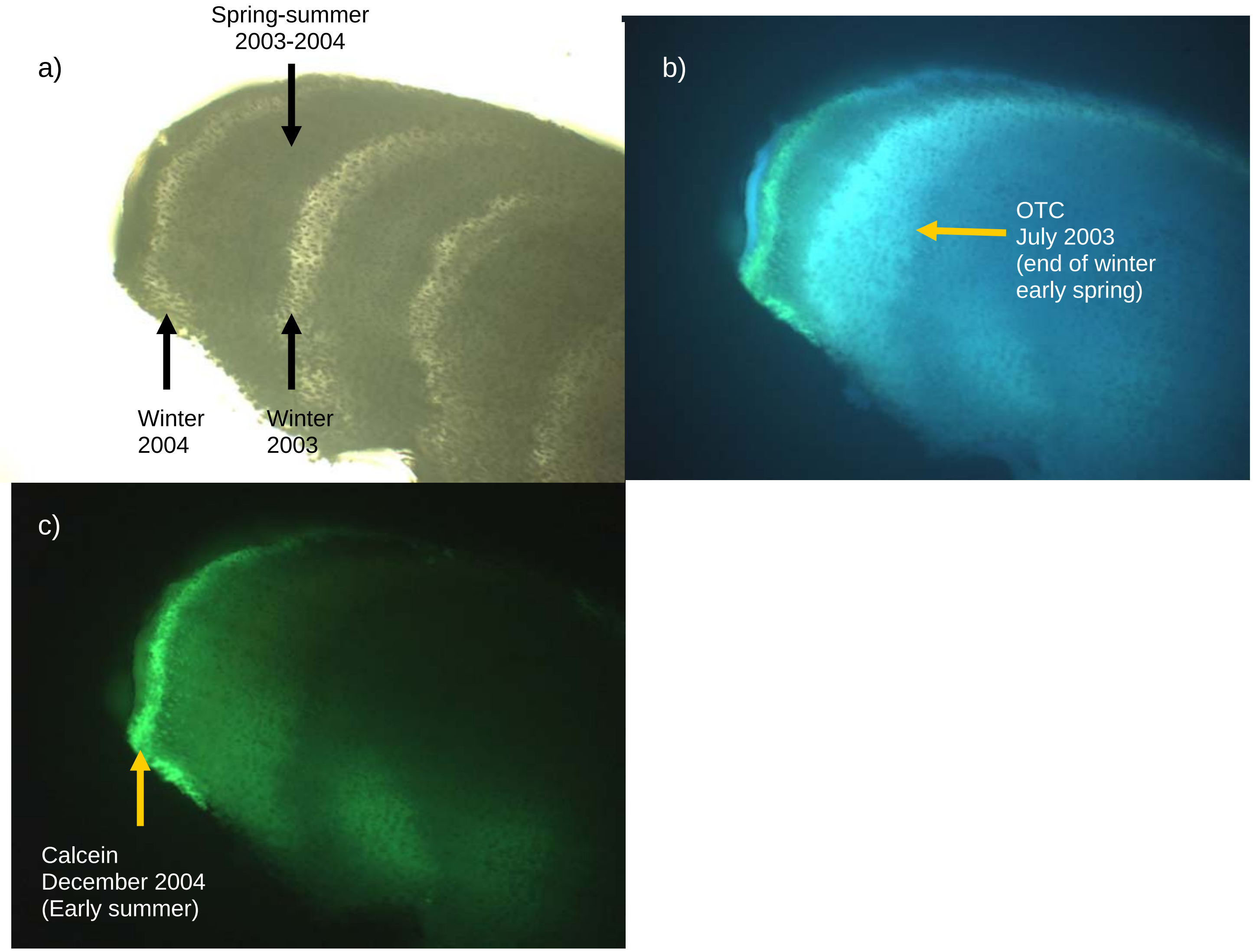


Figure 5. Transversal vertebrae section (a, b, c and d) showing growth bands formation in the *corpus calcareum*; female 906 mm TL (E4972) sacrificed January 2005.

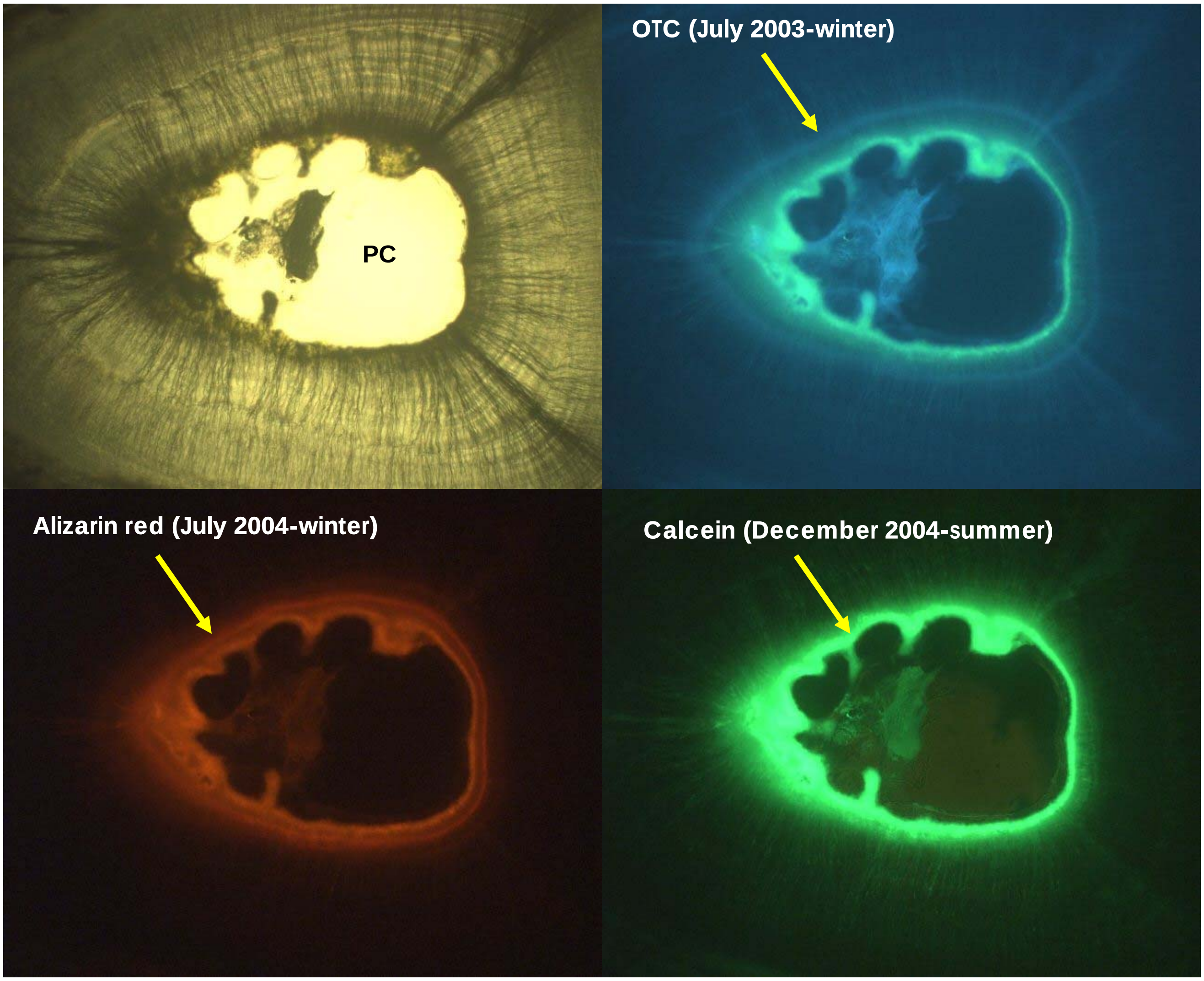


Figure 6. Transversal spine section showing inner trunk layer growth bands formation (female E4972, 906 mm TL sacrificed January 2005).

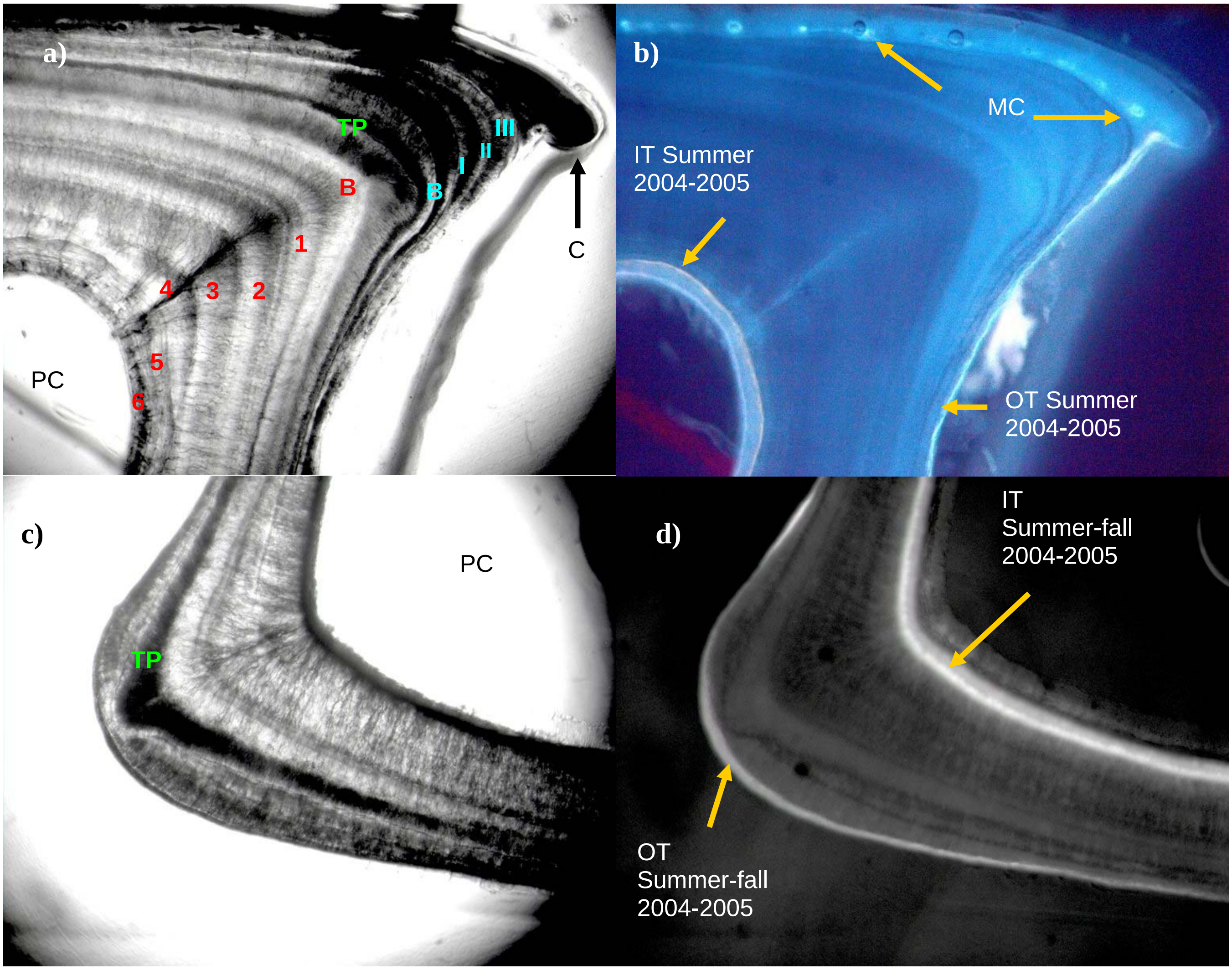


Figure 7. (a and b) Transversal section from the spines of a 574 mm TL male, 181 at liberty, showing the inner trunk (IT) growth bands (red Arabic numbers) and outer trunk (OT) growth bands (blue roman numbers) formation. (c and d) Transversal section from a spine of a 430 mm TL male, 160 days at liberty, showing the inner and outer trunk formation at the level of the base of the spine. Mantle canals (MC), birth mark (B), trunk primordium (TP), pulp cavity (PC) and cap (C) are shown.

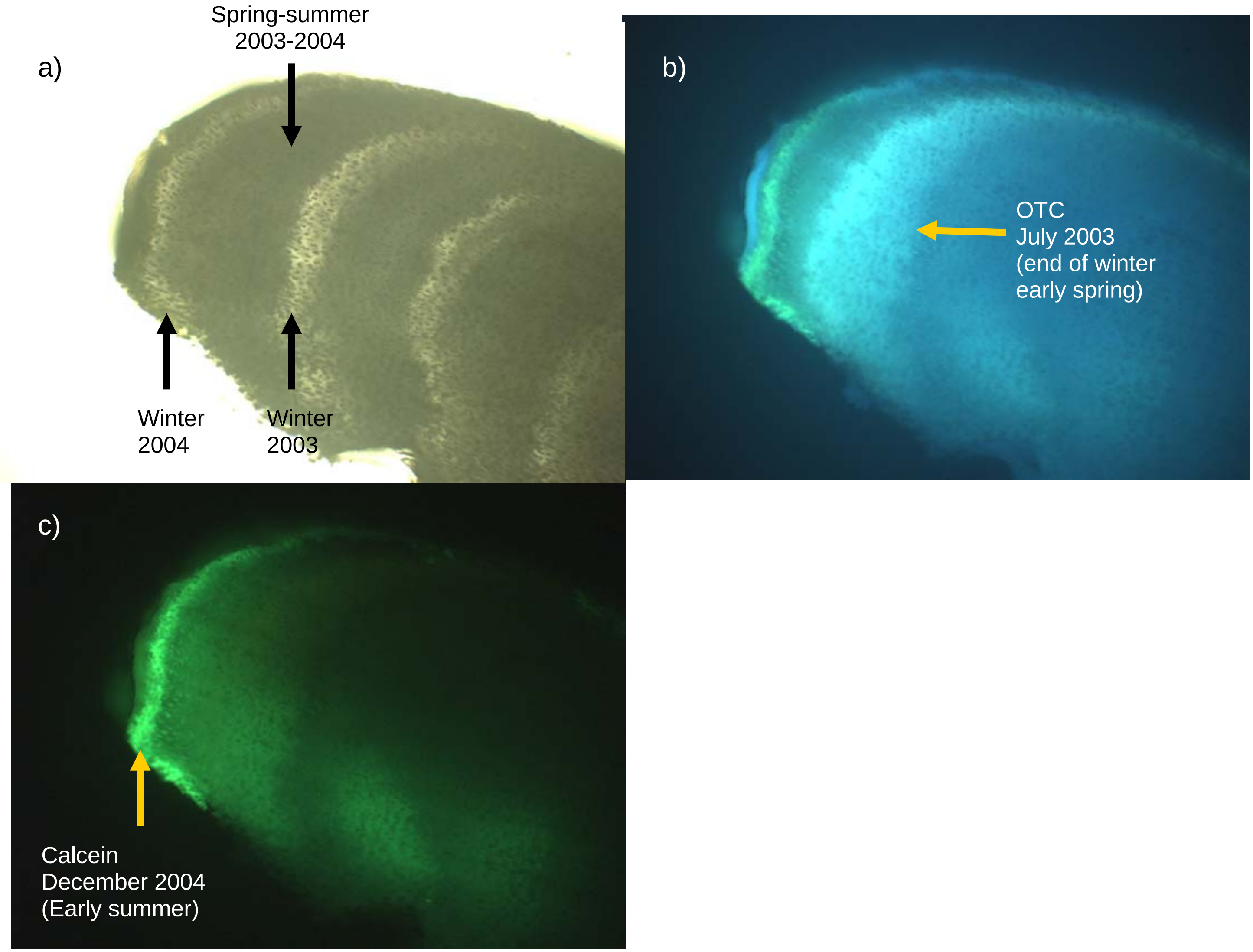


Figure 5. Transversal vertebrae section (a, b, c and d) showing growth bands formation in the *corpus calcareum*; female 906 mm TL (E4972) sacrificed January 2005.

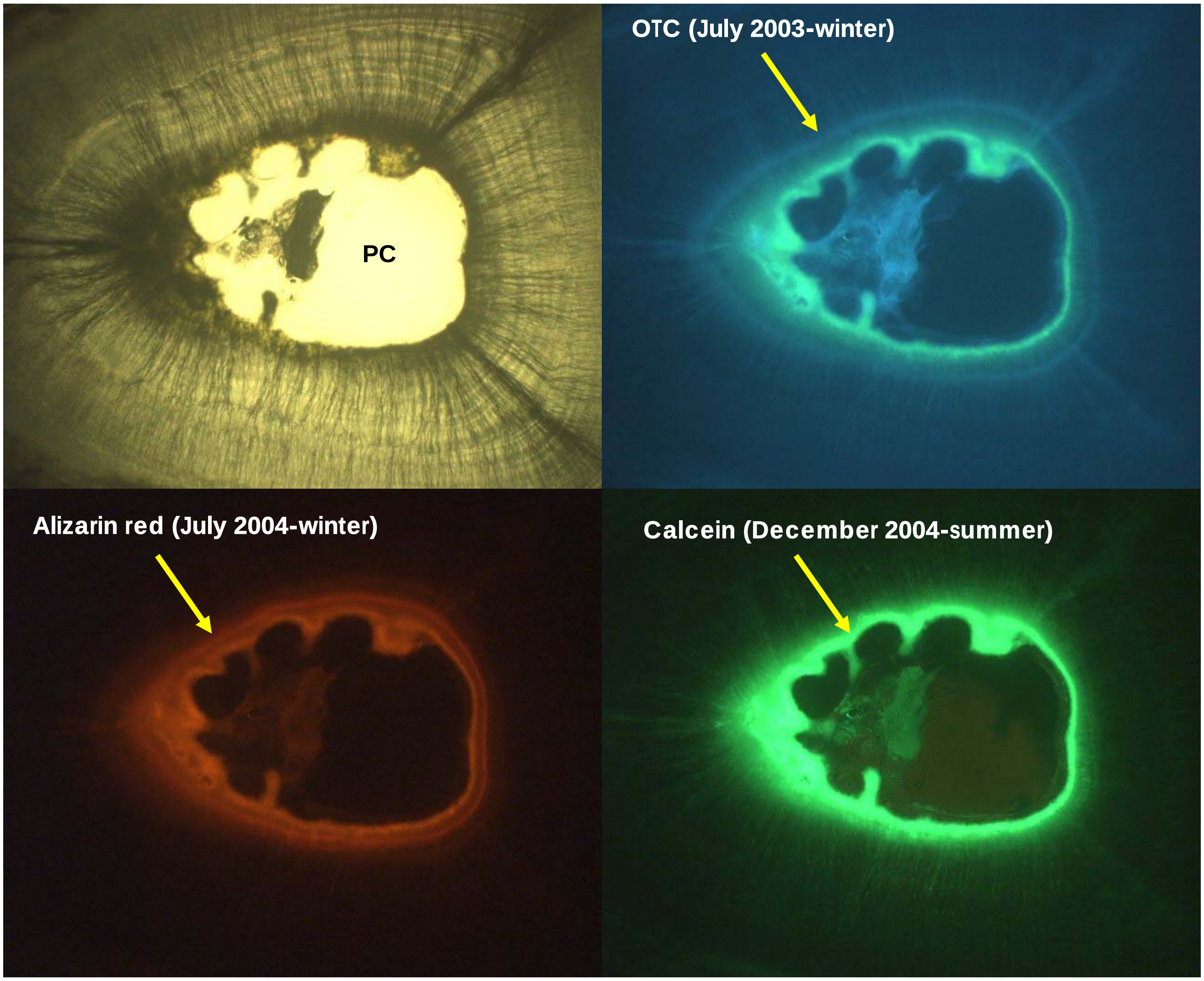


Figure 6. Transversal spine section showing inner trunk layer growth bands formation (female E4972, 906 mm TL sacrificed January 2005).

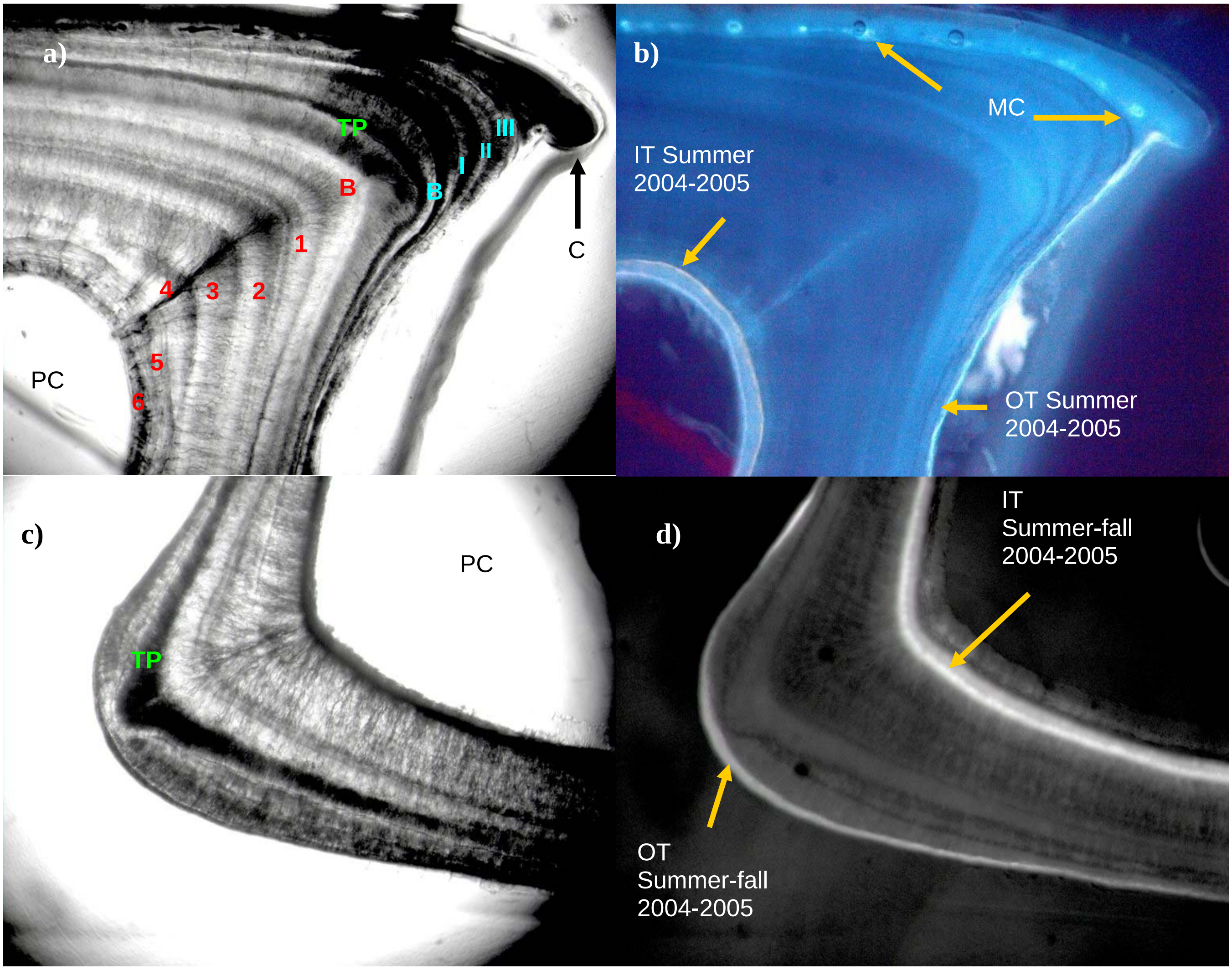


Figure 7. (a and b) Transversal section from the spines of a 574 mm TL male, 181 at liberty, showing the inner trunk (IT) growth bands (red Arabic numbers) and outer trunk (OT) growth bands (blue roman numbers) formation. (c and d) Transversal section from a spine of a 430 mm TL male, 160 days at liberty, showing the inner and outer trunk formation at the level of the base of the spine. Mantle canals (MC), birth mark (B), trunk primordium (TP), pulp cavity (PC) and cap (C) are shown.

Use of stochastic models to estimate the growth of *Heterodontus portusjacksoni* off eastern Victoria, Australia

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Three stochastic models based on the reparametrization of the von Bertalanffy growth model (VBGM) to take account of length-at-age heterogeneity, and the deterministic VBGM, were used to estimate the growth of *H. portusjacksoni* off eastern Victoria, Australia. The stochastic models incorporate random variation of the von Bertalanffy growth coefficient (*k*) using three different probability distribution functions (*pdf*) (Weibull, gamma and log-normal). Age estimations of 183 specimens (79 females and 104 males), obtained by counting the growth-increment bands in the inner trunk dentine layer of the dorsal-fin spines, were incorporated into the models. The species is relatively long-lived (maximum estimated age of 35 years for females and 28 years for males) and slow growing, but with rapid growth during the early stages of life. All stochastic models provided similar growth curves. Kullback´s information mean, however, indicated that the stochastic model assuming log-normal distribution fitted the length-at-age data better for both females and males than the models assuming gamma or Weibull distributions. The χ^2 likelihood ratio test indicated that female and male growth curves were different. Females tend to be larger than the males at any age greater than 6–8 years.

Key words: Chondrichthyans, growth, stochastic modelling.

INTRODUCTION

The description of somatic growth is a basic problem in population biology (Francis, 1988a). Growth rate is essential for some dynamic population models useful in determining sustainable yields of exploited species, such as yield per recruit models (Francis and Francis 1992). Age and growth also provide the base for the estimation of other important population parameters, such as mortality rate and longevity, necessary for assessment and management of a population (Natanson et al. 2002). Some biological variables (proportion of population mature or in maternal condition, litter size, mass) are commonly expressed as a function of the length of fish, but their expression as a function of age is necessary for demographic and other standard assessment models. Thus, confident estimates of population parameters that depend on age and growth, and confident demographic and fishery assessment using some particular methods depend on accurate determinations of age and reliable estimates of somatic growth rates.

Several functions have been developed to describe the somatic growth of fish, of which the von Bertalanffy (1938) growth model (VBGM), adapted posteriorly to fisheries by

Beverton and Holt (1957), is the most commonly adopted (Cailliet and Goldman 2004). The VBGM derived from the analysis of the physiological process involved in organic growth, thorough the relationship between anabolism and catabolism (von Bertalanffy 1938). Another convenience of the VBGM is its wide use, allowing comparisons with growth curves from other populations. However, the usefulness of this equation has been questioned because the values of two of its parameters (L_∞ and t_0) inevitably fall outside the range of data (Francis 1988a, b; Francis and Francis 1992), because of its limitations to describe growth if length-at-age data are not extensive to demonstrate asymptotic growth (Knight 1968; Francis 1988b), and because of its unsuitability to describe increment data from tagging experiments (Francis 1988a). To provide a more flexible and biologically comprehensive representation of growth, a stochastic variation of the VBGM has been developed (Troynikov 1998). This stochastic approach can explicitly account for both heterogeneity in length-at-age and measurement error by incorporating random variation in one or more of its parameters.

It is often claimed that chrondrichthyan species have slow somatic growth rates, but a wide range of growth coefficients among several species of this group indicates growth rates are highly variable (Cailliet and Goldman 2004). Heterodontid sharks have comparatively slow growth among chondrichthyan species. Observations of captive Port Jackson sharks (*Heterodontus portusjacksoni*), for example, indicate that juveniles grow 5−6 cm per year and adults grow 2−4 cm per year, and that males mature at 8−10 years and females mature at 11−14 years of age (McLaughlin and O´Gower 1971). However, no attempt has been made to determine growth parameters from ageing animals caught from the wild. In the present study, growth estimates are provided for *H. portusjacksoni* from Eastern Victoria, Australia, based on age estimations from growth-increment bands counted in the inner trunk dentine layer of dorsal-fin spines and taking account of length-at-age heterogeneity.

MATERIALS AND METHODS

FIELD SAMPLING AND AGE DETERMINATION

Specimens of *Heterodontus portusjacksoni* were caught by professional fishers in Far-Eastern Victoria (Mallacoota and Point Hicks) using gillnets of 6½-inch mesh-size. The first dorsal-fin spine was taken from each of 200 sharks (100 females and 100 males) for age estimation. For sharks where the first spine was extensively damaged, the second dorsal-fin spine was used, as both structures have been shown to provide similar age estimates (Tovar-Avila 2006). The 200 sharks were randomly sampled from ~400 sharks collected in the region, except for the largest and smallest animals, which were selected to include the minimum and maximum lengths.

Growth-increment bands on the inner trunk dentine layer of dorsal-fin spines were used to estimate the age of the specimens because of their precision, accuracy and practicality of use (Tovar-Avila 2006). The dorsal-fin spines were cleaned with a scalpel and washed in tap water. After cleaning, the spines were air-dried and stored in labelled paper envelopes. Transverse sections of the spines (~300 μm thick), at the level where the pulp cavity remains opened, were cut using a lapidary saw (Gemmasta®) after embedding the structures in polyester resin. The sections were mounted on glass microscope slides and sealed with cover slips.

A growth-increment band (comprising a pair of translucent and opaque zone) is formed annually in the inner trunk dentine layer of the dorsal-fin spines, with the first band corresponding to the birth mark (Tovar-Avila 2006). Two sets of counts of the growth-increment bands were made under a dissecting microscope for each sample. The counts were undertaken with a minimum of one month between them to avoid the second count being influenced by the first. Where two counts disagreed, a third count was made and a number of growth-increment bands was accepted where two of the three counts agreed. Where all three counts disagreed, but the difference in counts was low (Average percent error between counts of the sample, APE<1%), the sample was analysed again to assign the most probable number of growth-increment bands. Samples where all three counts disagreed and difference in counts was high (APE>1%) were rejected from further analysis. The readability of each section was ranked according to the clarity of growth-increment bands using the readability scale of Officer *et al.* (1996) (Table I). Only age estimates from dorsal-fin spines with a readability score ≤3 were included in the analysis.

The total age of sharks was determined from the number of band counts and the date of capture. Because *H. portusjacksoni* eggs commonly hatch during winter (end of June–end of August in the Southern Hemisphere), 1 July was arbitrarily set as the date of birth for all sharks, and all ages were adjusted by julian day (day after 1 January) of capture. The age of a shark (in years) was then calculated as the number of complete translucent zones (followed by an opaque zone) less one (birth band) plus Julian day divided by 365. For those sharks caught during the period from 1 January to 30 June, Julian day was adjusted by adding 180 days. For those sharks caught during the period from 1 July to 31 December Julian day was adjusted by subtracting 180 days.

GROWTH MODELS

Growth was determined using three stochastic VBGM (Troynikov 1998, 1999) based on parametrization of growth heterogeneity on length-at-age data. The models, in the form $f_l(x,t)$, representing the distribution of shark length (l) at age t, incorporates random variation of the von Bertalanffy growth coefficient (k) using three different probability distribution functions (*pdf*) (Weibull, gamma and log-normal). These *pdf*s were selected because they are the most commonly used for the description of positively distributed continuous variables (Troynikov and Gorfine 1998) (See Troynikov and Walker 1999 for each *pdf* parameter details). The mathematical expectation of the growth coefficient ($E[k]$) of the VBGM and its coefficient of variation ($CV[k]$), as a characteristic of heterogeneity in the population, were calculated with each model (each *pdf*). The distribution of length-at-age, and variation among age classes, can be represented by quantiles at age (Q_pt), where p is the probability corresponding to $f_l(x,t)$.

The goodness of fit of the models (M) to the data was compared by using the Kullback´s mean information integral Δ(M1,M2). If $\Delta < 0$ then model M2 fit the length-at-age data better. Although this method does not test statistical hypothesis, it allows for comparisons between models to select the *pdf* or the growth parameters that best fit the data (Troynikov and Walker 1999).

Growth was also estimated using the traditional deterministic VBGM, described by the equation

$$L_t = L_\infty\left(1 - \exp^{-k(t-t_0)}\right),$$

where L_∞ is the asymptotic average maximum length, k is the growth coefficient, and t_0 the hypothetical age when length equals zero.

Length at age 0 (L_0) was calculated for all the stochastic and deterministic models and compared with the length at hatching reported in the literature for the species.

Growth parameters estimated for males and females were compared by a chi-squared (χ^2) likelihood ratio test (Kimura 1980), defined as

$$\chi_k^2 = -N \times Ln\left(\frac{RRS_\Omega}{RRS_\omega}\right)$$

where k is the degrees of freedom, N is the total number of observations from both curves combined, RRS_Ω is the total sum of squared residuals derived from fitting both curves separately, and RRS_ω is the total sum of squared residuals derived from fitting the curve to the combined set of data. Likelihood ratio test is based on statistics having an asymptotically χ^2 distribution, providing a general method for the statistical comparison of growth curves.

The parameters and percentiles of the stochastic VBGM, and the parameters of the deterministic VBGM were estimated by maximum log-likelihood using a FORTRAN computer program (Developed by V. Troynikov, Primary Industries Research of Victoria Queenscliff Centre, Victoria, Australia). The Kullback´s mean information integral and the chi-squared likelihood ratio test were estimated using this computer program as well.

RESULTS

A total of 183 sharks were aged and used for growth estimations (79 females and 100 males). Female ages ranged from 3 (510 mm TL) to 35 (1190 mm TL) years, whereas male ages ranged from 2 (328 mm TL) to 28 (1033 mm TL) years. The largest specimens were not the oldest (1210 mm TL at 25 years old and 1080 mm TL at 18 years old for females and males, respectively).

The three stochastic VBGMs, based on Weibull (GW), gamma (GG) and log-normal (GL) *pdfs* for *k*, provided similar growth parameters (Table II). The mathematical expectations of *k* (*E[k]*) of the stochastic models ranged 0.057–0.059 for females and 0.061–0.075 for males. The *CV[k]* ranged 19–21% in both females and males, indicating that *E[k]* from all the models provide a similar description of the distribution of length-at-age in the population. The parameters L_∞ of the stochastic VBGMs ranged 1337–1364 mm TL for females and 1125–1197 mm TL for males. The parameter t_0 ranged 5.178–5.294 for females and 4.944–6.241 for males.

The deterministic VBGM provide different growth parameters and curves for females (L_∞= 1242, k= 0.070, and t_0= 3.86) and males (L_∞= 1080, k= 0.084, and t_0= 4.086) (Table II and Fig. 1).

All stochastic (25–95% quantiles) and deterministicVBGMs provided estimates of L_0 above the reported length at hatching, 230–240 mm TL(McLaughlin and O´Gower 1971; Last and Stevens 1994; Compagno 2001). The 5% quantiles for the stochastic VBGMs, however, were close to the reported length at hatching, and in the case of GW for females between the range of reported length at hatching (Table III).

The Kullback´s information mean (Δ) obtained between the GG and GL models was lower than Δ between the GW and GG for both females and males, and both were lower than Δ between the GW and GL models (Table IV). This indicates that the GL provides the best fit to the length-at-age data (Fig. 1), and the GW the worst. However, Δ between the GW and GG, and between the GW and GL models were relatively small.

The χ^2 likelihood ratio test indicated that the female and male growth curves were statistically different for all the stochastic models (P<0.005 in all cases) (Table V); females tend to be larger than the males for any age greater than 6–8 years.

Cross sections of the probability density distribution of length-at-age indicate variability is similar for early ages, but narrower for age 30 for females and age 25 for males (Fig. 3). The distribution of length-at-age was slightly wider for females than for males.

DISCUSSION

Growth curves of *Heterodontus portusjacksoni* show the species presents relatively slow growth compared with other shark species. Growth is more rapid, however, during the early years of life than after reaching maturity in *H. portusjacksoni*. Female *H. portusjacksoni* grow more slowly and reach larger sizes than males of the species, as use to happened in most chondrichthyan species (Cailliet and Goldman 2004). The difference between female and male growth starts after reaching 6–8 years, which are consistent with the age-at-maturity estimates for males (McLaughlin and O´Gower 1971; Tovar-Avila 2006). The growth curves estimated in the present study cannot be compared with growth curves for species of the same taxon because of the lack of studies on age and growth of other heterodontid sharks, but the results of the present study are consistent with observations of growth on *H. portusjacksoni* held captive (McLaughlin and O´Gower 1971).

Direct comparison of individual von Bertalanffy parameters between populations or species is meaningless, because k, L_∞ and t_0 are highly correlated, and quite different parameter combinations can produce similar curves, being better to compare the actual growth curves (Francis and Francis 1992). Nevertheless, growth parameters can serve as an early flag of populations at risk (Musick 1999). Growth coefficients (k) vary in other sharks from 0.03 in species considered to have slow growth, such as *Rhincodon typus* and some *Squalus* spp, to

1.34 in species considered to have fast growth, such as *Rhizoprionodon taylori* (Cailliet and Goldman 2004). *H. portusjacksoni* presented low values of *k* for the deterministic model (0.07 for females and 0.084 for males).

Although $f_l(x,t)$ for maximum age *t* can be considered as an approximation to the distribution of maximum length in the population (Troynikov and Walker 1999), L_∞ estimated with all the stochastic models was lower than the maximum reported size for the species (~1,500 mm TL) (Last and Stevens 1994). This result could be related to the smaller size of sharks caught because of selectivity of the fishing gear, as gillnets are highly length-selective (Kirkwood and Walker 1986). Another explanation of L_∞ being lower the maximum length reported in the literature could be that the eastern Victoria population presents a maximum length lower than other populations of the species. The presence of several populations in Australian waters has been suggested from previous tagging studies (O'Gower and Nash 1978), whereas differences found in the reproductive biology within sharks from different regions off Victoria suggest the presence of at least two populations in the region (Tovar-Avila 2006).

In the case of the deterministic model, L_∞ is not the maximum size of the population but the predicted mean length at age ∞. Still, the deterministic L_∞ was far from the maximum length of the species, but close to the maximum length observed for both females and males. The lower L_∞ obtained from the deterministic VBGM can reflect the limitations of this approach and its inappropriate fit to some data (Knight 1968; Francis 1988b; Francis and Francis, 1992), but could be related in the present study to the smaller size of sharks caught because of selectivity of the fishing gear as well. It has been shown that the deterministic approach tends also to underestimate the value of k (Sainsbury 1980) but in the present study, however, the deterministic model tended to produce higher values of k.

The overestimation of L_0 by all stochastic and deterministic models might be related to the lack of small size individuals size in the samples, close to the hatching size. The use of gillnets to obtain the samples in this region limited the sizes in the sample. The stochastic models intervals allowed, however, estimates of L_0 close, or identical in the case of GW for females, to the reported length at hatching (5% quantiles) showing one of the conveniences of these approaches.

Stochastic growth models have several advantages over deterministic models. Stochastic growth models allow the description of heterogeneity in length-at-age, providing a more complete representation of growth in a population (Troynikov and Walker 1999). Growth heterogeneity is the result of natural variability in a population due to endogenous (genetic) and exogenous (environmental) factors, methodological error and sampling bias. Ignoring such heterogeneity can result in biased estimates of the growth parameters (Sainsbury 1980). Sampling bias can be a major problem to obtain appropriate data for determining growth (Francis and Francis 1992); this bias is particularly marked for gillnet mesh-size selectivity where mid-size mesh sizes more selectively catch large young fish and small old fish (Kirkwood and Walker 1986; Walker et al. 2005). If large adults evade capture, the mean length of the older age groups will be underestimated, L_∞ will be too low and k too high as these two parameters are highly correlated (Francis 1988b; Francis and Francis 1992).

Growth variability has been addressed by other authors by estimating the VBGM parameters for individual fish (Sainsbury 1980; Francis 1988a), but these methodologies are limited because of the assumption that the growth parameters of each individual are fixed, and retained throughout life. The models used in the present study treat instead individual histories of size as a random process and length at any given age is represented by a distribution (length-at-age heterogeneity).

Another advantage of stochastic growth models is that they incorporate variation in the form of a *pdf*, providing flexibility to explore different *pdfs*, and overcoming the need to impose an assumption on the particular form of variation in growth; e.g. variance in length constant or proportional with length in the gamma *pdf* (Francis 1988a) or constant variance with age assumed for most models. In contrast to models assuming a normal distribution (e.g. deterministic VBGM), the stochastic models used in the present study have *pdfs* with no negative tails in the size at age distribution, avoiding unrealistic representations of growth (Troynikov 1998; Troynikov and Walker 1999).

It is concluded that *H. portusjacksoni* is a relatively slow growing species, in which growth is better described by a stochastic approach of the VBGM, as this has the advantage of explicitly accounting for heterogeneity in length-at-age data.

Acknowledgments

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Table I. Readability score (modified from Officer et al. 1996).

Score	Description
1	Increment count unambiguous with exceptionally clear increments
2	Increment count unambiguous but increments of diminished clarity
3	Two increment counts possible but indicated count is most likely
4	More than two interpretations possible; increment count is best estimate
5	No increment count possible; unreadable

Table II. Parameter estimates of the stochastic models and the traditional deterministic von Bertalanffy growth model, for male and female *Heterodontus portusjacksoni* in Far-Eastern Victoria, Australia. CV(%), coefficient of variation expressed in percentage. (CV) for *E(k)* represents heterogeneity in the population rather than statistical error. η and α are the parameters of the Weibull *pdf*, ρ and λ are the parameters of the Gamma *pdf*, μ and σ are the parameters of the Log-normal *pdf*. ne, not estimated.

		Females		Males	
Model	Parameter	Estimate	CV(%)	Estimate	CV(%)
Weibull	$L\infty$ (mm)	1364	50	1197	40
	$E(k)$ (year^{-1})	0.057	(21)	0.061	(20)
	t_0 (year)	5.178	26	6.241	19
	η	5.610	ne	5.645	ne
	α	0.0612	ne	0.0658	ne
Gamma	$L\infty$ (mm)	1348	64	1138	54
	$E(k)$ (year^{-1})	0.058	(20)	0.072	(20)
	t_0 (year)	5.340	27	5.237	17
	ρ	0.0582	ne	0.07207	ne
	λ	0.00013	ne	0.00020	ne
Log-normal	$L\infty$ (mm)	1337	71	1125	67
	$E(k)$ (year^{-1})	0.059	(19)	0.075	(20)
	t_0 (year)	5.294	27	4.944	17
	μ	−2.855	ne	−2.606	ne
	σ	0.1904	ne	0.2016	ne
Deterministic	$L\infty$ (mm)	1242	54	1080	ne
von Bertalanffy	k (year^{-1})	0.070	189	0.084	ne
	t_0 (year)	3.860	343	4.086	ne
	sample size	79		100	

Table III. Estimates of length at age 0 (L_0) for *Heterodontus portusjacksoni* in Eastern Victoria, Australia, using three stochastic von Bertalanffy growth models (VBGM) and its deterministic version.

Model	Quantiles (%)	Females	Males
		L_0 estimate (mm)	
Weibull	5	232	258
	50	350	382
	95	436	470
Gamma	5	263	263
	50	356	354
	95	460	454
Log-normal	5	267	259
	50	351	344
	95	456	448
Deterministic VBGM		293	314
Length at birth reported		230–240	

Table IV. Kullback´s information mean Δ(M1,M2) for comparisons between the stochastic growth models for *Heterodontus portusjacksoni* in Eastern Victoria, Australia. If Δ <0 then M2 fit the data better. CV(%), coefficient of variation expressed as percentage.

	Females		Males	
	Δ	CV(%)	Δ	CV(%)
Weibull-Gamma	-0.0584	30	-0.0932	21
Weibull-Log normal	-0.0843	33	-0.1070	24
Gamma-Log normal	-0.0259	44	-0.0139	42

Table V. Chi squared (X^2) likelihood ratio test for growth curves of female and male *Heterodontus portusjacksoni* in Eastern Victoria, Australia, using three different growth models. *d.f.* degrees of freedom; *P*, probability of statistical significance.

Model	*d.f.*	X^2	*P*
Weibull	4	32.283	< 0.005
Gamma	4	75.668	< 0.005
Log-normal	4	28.755	< 0.005

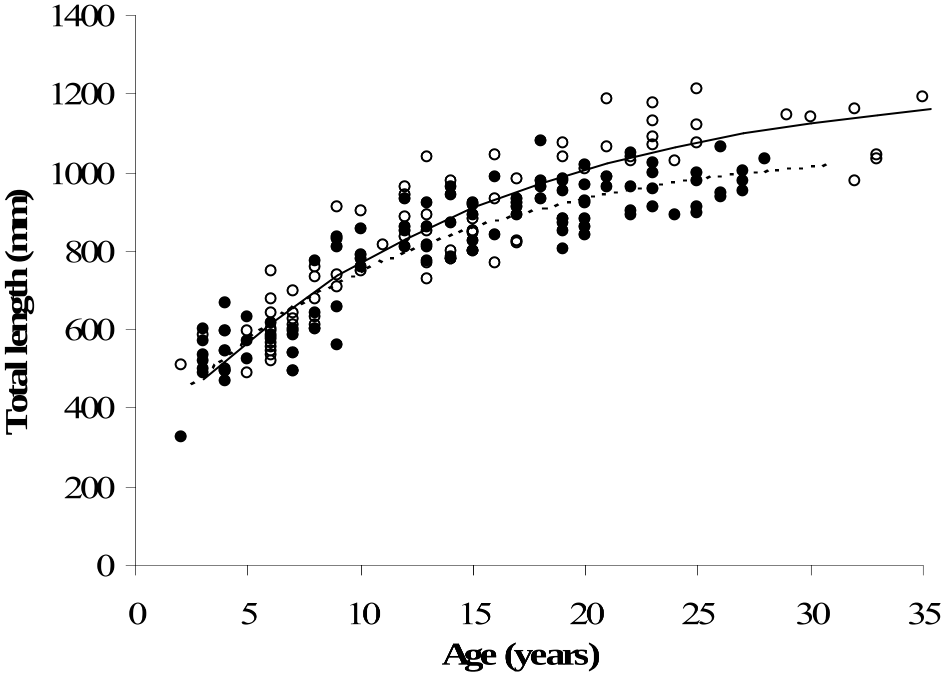
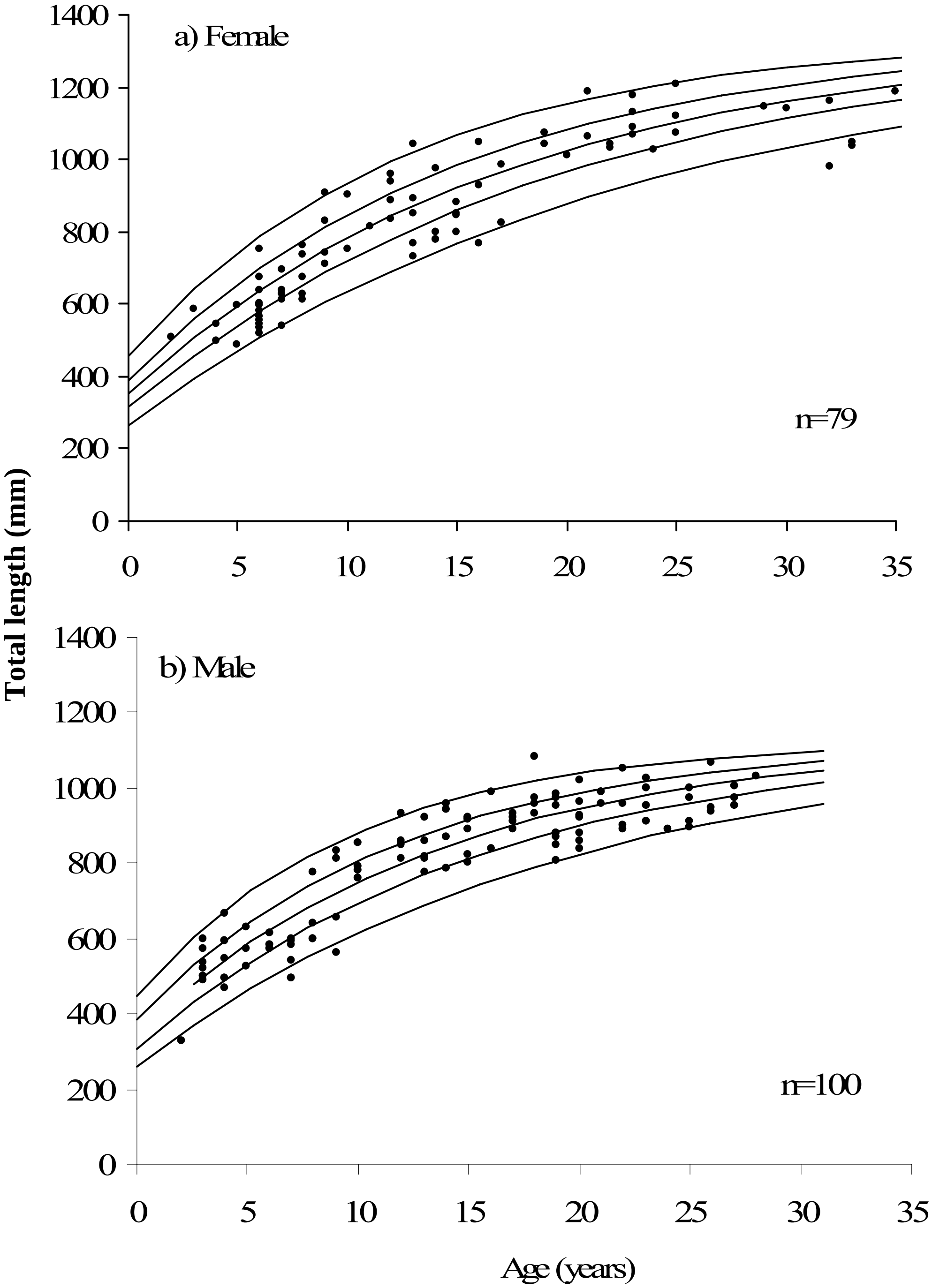


FIG. 1. Age versus total length for the deterministic von Bertalanffy growth model for *Heterodontus portusjacksoni* females (○) (——) and males (●) (- - - -) in Eastern Victoria, Australia.



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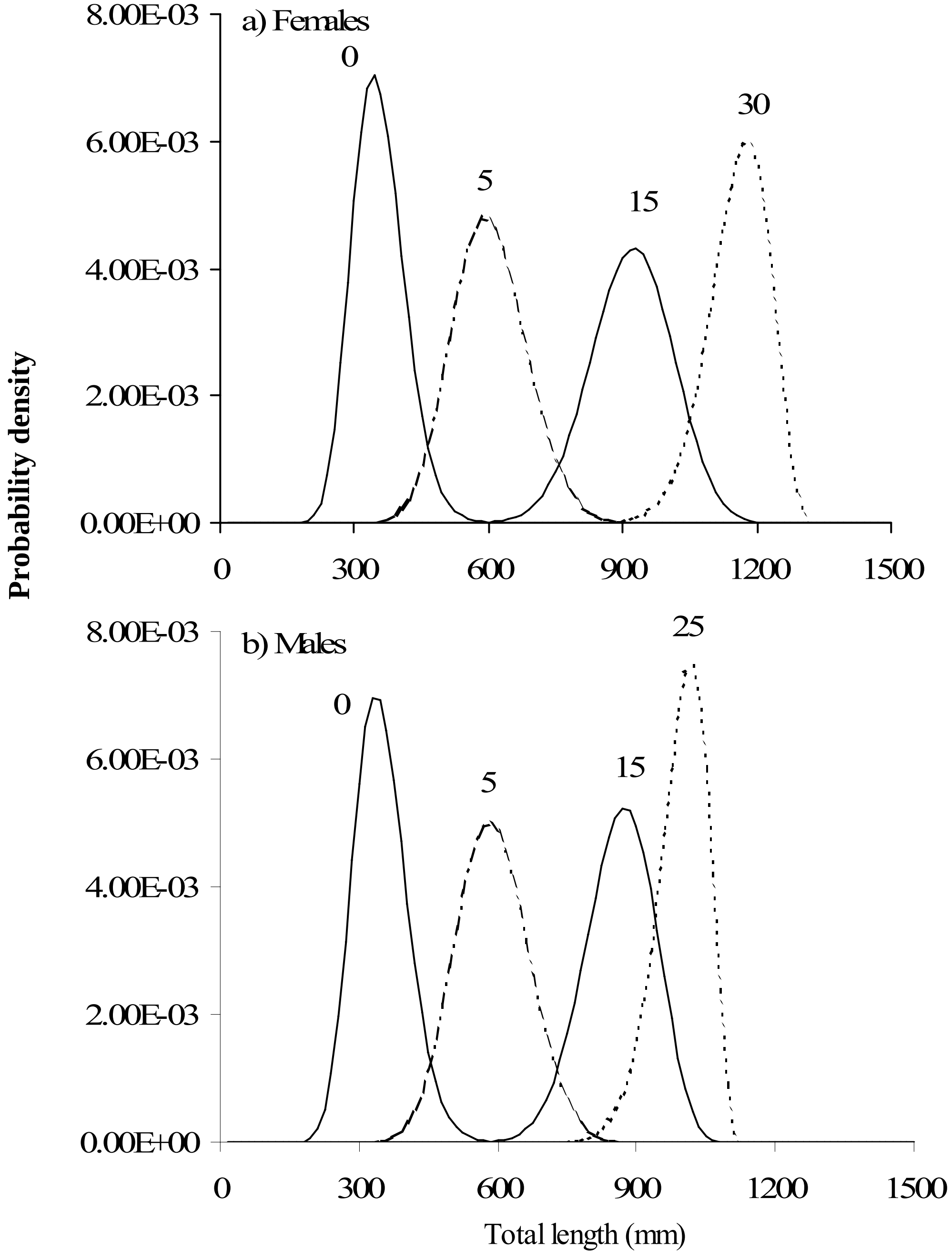

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13. Management measures

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13.1 INTRODUCTION

Fisheries management can be viewed as an assemblage of restrictions on fishing or, alternatively, viewed with positive connotations as bestowing use rights for harvesting fish to an individual, company, group or community. With use rights go the obligation to apply those rights in a responsible manner.

In allocating fishing rights, clear objectives need to be set for a fishery. These objectives will relate to sustainable use of the resource, provision of food and other products, economic return to the community, welfare of fishing communities, biodiversity conservation and maintenance of the structure and function of ecosystems. The mix of objectives for any fishery will inevitably change with community attitudes and with stage of development depending on whether the fishery is evolving from a traditional to an artisan fishery or from an artisan to an industrial fishery. Compromises are inevitable in successfully addressing competing social, political, legal, economic and biological objectives.

Fisheries impacting populations of chondrichthyans (sharks, rays and chimaeras) require careful management. Where excess fishing capacity occurs, mechanisms need to be established to reduce capacity to levels commensurate with the biological productivities of the harvested species to ensure sustainable and rational use of the resources. Similarly, where bycatch species are depleted or threatened, then steps need to be taken to manage and, if necessary, provide special protection to those species for biodiversity conservation. Critical habitats need to be protected and, where affected by fishing or other human activities, restored. At a broader level, trophic interactions and the effects of fishing need to be understood and if necessary managed to ensure that the resilience of ecosystems are not impaired.

The present Section briefly characterizes fisheries that affect populations of chondrichthyan species and identifies those features of their biology that can cause their populations to be sensitive to the effects of fishing. It outlines the elements of fishing mortality and how these need to be understood when considering gear restrictions or constructing more environmentally benign gear for conservation and management of this group of animals. The Section develops a method for rapid assessment of risk to identifying species most in need of precautionary management. It also describes the outcomes of complex political processes culminating in the International Plan of Action for the Conservation and Management of Sharks and describes the jurisdictional and institutional frameworks required for administration, consultation, monitoring, research, assessment and surveillance in fisheries. The tools of fisheries management are presented here in the framework of use rights and restrictions imposed through technical measures. For chondrichthyan animals, special attention is required to protect newborn and young juveniles and maternal animals for species that have nursery, pupping and mating grounds, or migration lanes. The advantages of prescribing in law the form in which these animals can be landed are also discussed.

The terminology adopted mostly follows the Code of Conduct for Responsible Fisheries developed under the auspices of the Food and Agriculture Organization of the United Nations (FAO, 1995). The term "catch susceptibility" is adapted from the scientific literature (Stobutzki, Miller and Brewer, 2001; Stobutzki *et al.*, 2002) for the purpose of the present chapter. In addition, a distinction is made between the terms "fishing area closure" and "marine protected area". This distinction is made to distinguish area closures designed to meet fishery-management objectives of ensuring sustainable use of a resource, biodiversity conservation, amelioration of ecological impacts of fishing and reduction of interference with other human activities (e.g. shipping and recreation) from area closures designed to meet other community objectives. The concept of a fishing area closure, which is an essential management tool for managing animals of low productivity such as chondrichthyans, is extended to promote the concept of "regional fisheries management".

13.2 FISHERIES, BIOLOGY AND ASSESSMENT OF CHONDRICHTHYAN SPECIES

13.2.1 Fisheries affecting chondrichthyan species

The harvest of animals for products from shark and other chondrichthyan species predates recorded history. Every part of these animals has been used for some purpose. Depending on the region of the world, shark meat is an important food consumed fresh, dried, salted or smoked. The demand for fins of sharks has grown rapidly in recent years such that they are now among the world's most expensive fishery products. Similarly, the demand is rising for shark cartilage and other products for medicinal purposes. In some fisheries, only the meat is retained, while the rest of the animal is discarded. In other fisheries, only the fins, or liver or skin is retained; few fisheries utilize all parts of the animals.

The number of shark species targeted is small compared with the number of species of teleosts and many of the invertebrate phyla harvested. This has resulted in a lack of studies of sharks and inappropriate stock assessment techniques being applied to these animals. Most of the shark catch is taken by fishers targeting teleost species, which results in most of the catch being reported as unidentified shark or mixed fish or not reported at all. In addition, sharks can be difficult to identify to species level, particularly given the need to behead and eviscerate sharks at sea to reduce spoilage rates of the meat and the fishers" preference to remove fins at sea. Taxonomic problems need to be resolved, particularly for batoids, before effective monitoring, research and management can be achieved. This lack of species identification for catches and lack of information on fishing effort means basic data for fishery stock assessment are currently available for only a few species (Walker, 1998).

Although the overall number of species harvested is relatively small, sharks are captured with a wide variety of fishing gear and vessels. Sharks are mostly taken by gillnet, hook or trawl in industrial and artisanal fisheries. Small amounts are taken in traditional and recreational fisheries, including game fishers and divers, and by bather protection programs using beach gillnets and drumline fishing. There are several fisheries directed at one or a small number of species of sharks, but most sharks are taken in multispecies fisheries where the fishers tend to target more highly valued teleosts. In some fisheries, part or the entire shark catch is discarded. Shark fisheries can be classified as "coastal hook and gillnet fisheries", "demersal trawl bycatch fisheries", "deepwater bycatch fisheries", "pelagic bycatch fisheries" (primarily bycatch in tuna longline and purse seine fisheries) and "freshwater fisheries" (FAO, 2000).

Coastal hook and gillnet fisheries operate in regions of the continental shelf. Construction of the fishing gear depends on topography of the fishing grounds and on the available species mix of shark, chimaerid and teleost species. Much of the artisanal catch is taken by bottom-set longlines and by bottom-set gillnets, mostly constructed of monofilament webbing with some constructed of multifilament webbing. These gears take a variety of shark species and teleost species. In regions of narrow continental shelves where deep waters off the continental shelf are readily accessible, or in regions of broader continental shelves, the artisanal fleet uses surface-set longlines and driftnets to target pelagic sharks (FAO, 2000).

In demersal trawl bycatch fisheries, demersal trawl fisheries reduce stocks of dogfishes (*Squaliformes*), angel sharks (*Squatiniformes*), rays (batoids) and chimaeras (holocephalans). As in the high seas fisheries, much of the trawl bycatch of sharks and rays is discarded dead and often not reported. Fishery-independent surveys in several parts of the world show that many species of these groups have exhibited marked declines in abundance.

In deepwater bycatch fisheries, like many of the teleost species studied from the deeper and colder waters of the continental slopes, the deepwater dogfishes (notably the genera *Centrophorus*, *Centroscymnus*, *Etmopterus*, *Dalatias* and *Deania*) have particularly low productivity. The continental slopes are usually steep and the total area of associated seabed is small compared with the areas of the continental shelves and the abyssal plains of the oceans. As some species of dogfish are confined to particular depth-ranges on these slopes, the total area occupied by some of these species is small. Expansion of demersal trawl fisheries into progressively deeper water to target dogfish and high valued teleosts on the continental slopes in some regions of the world is placing several species at high risk of severe depletion. Already demersal trawling occurs on the continental slopes at depths exceeding 1000 m. Part of the catch is targeted or is bycatch taken by gillnets and hooks (Walker, 1998).

In pelagic shark bycatch fisheries, longline, purse seine and driftnet fisheries targeting tunas and tuna-like species on the high seas and in the Exclusive Economic Zones, through bilateral access agreements, take significant bycatch of sharks. Blue shark (Prionace glauca) is the main species caught and other species caught widely in lower quantities include Isurus oxyrinchus, Alopias supercilious, Carcharhinus falciformis, Carcharhinus longimanus and Lamna nasus (Bonfil, 1994; FAO, 2000).

In freshwater fisheries, shark species occurring in freshwater habitats are among some of the most threatened species. There are several reasons why these species are more vulnerable than those inhabiting marine waters. The amount of freshwater in rivers and lakes is small compared with the amount of seawater on Earth. The tropical rivers and lakes where freshwater species occur are mostly in developing countries with large and expanding human populations. These areas are more accessible to exploitation than marine waters. Freshwater habitats are also less stable than marine habitats in terms of water temperature, dissolved oxygen, clarity and water flow and these factors are gradually being changed through deforestation. Contamination of the water with toxicants from mining and agriculture, physical modifications to the waterways through dam construction and irrigation and inevitable changes to the flora and fauna in freshwater habitats are likely to alter them beyond the tolerance of some shark species. Several species of sharks and rays have declined such that they are now extremely rare (Compagno, 1984; Compagno and Cook, 1995).

13.2.2 Biological characterization of chondrichthyan species

Populations of shark and other chondrichthyan species tend to have lower reproductive rates and lower natural-mortality rates than populations of teleost and invertebrate species. Consequently, for many chondrichthyan species, only a small proportion of the population can be removed annually if the catches and populations are to remain sustainable. Such populations are said to have low biological productivity.

Harvested populations of these animals therefore require careful management and monitoring. Managers need to take a more precautionary approach to the management of fisheries that take sharks than they might to the management of fisheries based on teleost or invertebrate species. Late maturity, low fecundity and parturition cycles often exceeding one year provide for close stock-recruitment relationships, with relatively little inter-annual variability in response to environmental variation and for long stock recovery periods in response to overfishing.

There are directed fisheries for sharks in various parts of the world, but most species of shark are captured in multispecies fisheries directed at more productive and usually more highly valued teleost species. Harvest strategies designed to optimise economic and social benefits from these multispecies fisheries inevitably deplete the less productive shark and other chondrichthyan species unless strategies for reducing the catch of the less productive species can be developed and implemented. As fishing effort increases, characteristic and predictable changes occur in the fish assemblages. The number of large animals decline or disappear from the assemblage and are replaced by smaller animals. This results in a gradual drift towards shorter-lived, faster-growing species. This is accompanied by an initial increase and later a decrease in the number of species in the exploitable population although the number of fish actually appearing in the catch can increase to a maximum level.

In multispecies fisheries where the main target species are teleosts, sharks landed as nontarget species (byproduct) or caught and discarded (bycatch) might require "special management" to prevent severe depletion. Some species of shark are apex predators and naturally have comparatively small population sizes. Whereas some species have wide geographic distributions, others have restricted ranges falling within the full range of a fishery or the range of other anthropogenic influences. Some species have complex spatial stock structures, with critical habitats such as nursery, parturition and mating areas and migration lanes, which might need special protection (Walker, 1998).

The magnitude of change in many of the world's fisheries has not been well appreciated because most of the change occurred during the early developmental stages of the fisheries before surveys began and subsequent fisheries management has only been effective at stabilising fish stocks at low levels. Recent meta-analysis of large survey data sets from throughout the world indicates industrialized fisheries typically reduce community biomass by 80% during the first 15 years of exploitation, which inevitably leads to marked changes in coastal ecosystem structure and function. The analyses suggest that the global ocean has lost more than 90% of large predatory fish (Myers and Worm, 2003). This paints a bleak picture for the world's fish fauna and marine ecosystems in general, but given the biological characteristics of the chondrichthyan fauna, it can be expected that this group of animals is among the most severely affected. This is exacerbated in the open ocean for large predatory sharks, which, along with tunas, billfishes and sea turtles, tend to aggregate at distinct diversity hotspots associated with coral reefs, shelf breaks and sea mounts. These animals appear to be particularly vulnerable to targeting in latitudes 20-30° N and S where tropical and temperate species overlap (Worms *et al.*, 2003).

The failure to manage for sustainability at rational levels is primarily due to socio-political pressure for short-term gain in harvests and due to intrinsic uncertainty in predicting the harvest that can cause stock collapse. There is, nevertheless, a growing awareness of the need for a more holistic approach by considering multispecies interactions and influences of the physical environment to achieve sustainability through adaptive management (Botsford, Catilla and Peterson, 1997).

This requires an ecosystem approach to fisheries management, which integrates information from a wide range of disciplines and applies mathematical models to synthesize multiple processes at a wide range of spatial and temporal scales. Greater use of fishing area closures and moratoria can reduce risks to sustainability through application of the precautionary principle. Harvest refuges effectively protect a proportion of the exploited population and reduce uncertain assumptions about relationships between fishing effort, catch and biomass (Botsford, Catilla and Peterson, 1997). Exposing an entire population to exploitation without a sound understanding of the dynamics of the fishery can risk depletion, whereas fishing area closures can serve as a hedge against inevitable uncertainty (Lauck *et al.*, 1998). However, such areas provide insufficient protection alone because they are not isolated from all critical impacts; scales of fundamental processes, such as population replenishment, are much larger than the areas they can encompass. Fishing area closures need to be complemented by other management and conservation measures outside the closures (Allison, Lubchenco and Carr, 1998).

An ecosystem approach to fisheries management requires management over broad regions and across fisheries and away from single-species and single-fishery management that characterizes past and present practices. The approach involves monitoring all species affected by fishing and requires better understanding of the dynamics of fish movement and species interactions through food chains. Whereas complex models and comprehensive long-term monitoring data sets are required to reduce uncertainty, it is essential in the short-term to develop rapid assessment methods based on simpler data sets and judgement that can provide for interim management of species and ecosystems at risk.

13.2.3 Fishing mortality

In fishery models, fishing mortality rate for a harvested population is usually expressed as the product of the two quantities: fishing effort and catchability. Fishing effort can be quantified as the number of fishing vessels in a fleet, a measure of the amount of fishing gear deployed, amount of fishing time, or some other variable that is a mix of these variables. "Catchability" is the proportion of the exploited population taken by one unit of fishing effort and has a value in the range 0–1 for any age or size of fish. It is the product of three parameters, each of which also has a value in the range 0–1. The three parameters comprising catchability are "availability", "encounterability" and "selectivity"; i.e.:

catchability = availability x encounterability x selectivity

Availability is the proportion of the habitat area of a population fished by the fleet. A population with a habitat area extending well beyond the range of the fishing fleet has a low availability value. Conversely, a population with a habitat area that falls entirely inside the range of the fishery has a high availability value of one, unless parts of the habitat area are inaccessible to the fishing fleet.

Encounterability is the proportion of that part of the population available to fishery encountered by one unit of fishing effort. For any species, encounterability depends on construction of the fishing gear and on the biological characteristics of that species. Pelagic and semipelagic species that actively swim in the water column are more likely than less active species to encounter passive gears such as gillnets or longlines with baited hooks. These actively swimming species therefore have a higher encounterability to these gears than the less active species. For mobile gears such as demersal trawl, bottom-dwelling, sluggish species, such as angel sharks (Squatiniformes) and batoids have a higher probability of capture and therefore higher encounterability than the more powerful swimming species, such as the whaler and hammerhead sharks (Carcharhiniformes) and mackerel sharks (Lamniformes). Sixgill and sevengill sharks (Hexanchiformes), sawsharks (Pristiophoriformes), dogfishes (Squaliformes), catsharks, wobbegong and carpet sharks (Orectolobiformes) and horn sharks (Heterodontiformes) probably exhibit intermediate trawl encounterability.

"Selectivity" is the proportion of the animals encountering the fishing gear that is captured by the fishing gear. For any fishing gear, selectivity gives rise to a range of complex dynamics that relate features of the fishing gear to size of the fish captured. Selectivity by trawl nets for size of chondrichthyan animals is not well understood and hook-size selectivity for size of fish is weak. For gillnets, however, sharks of different sizes are not equally vulnerable to capture. Small animals swim through gillnets but become progressively more vulnerable to capture as they grow. After reaching the length of maximum vulnerability they then become progressively less vulnerable with further growth as they deflect from the meshes of the nets (Kirkwood and Walker, 1986). These size selectivity effects are stronger for fusiform-shaped sharks than for more dorsoventrally-flattened species or for species with protruding structures such the heads of hammerhead sharks, the rostral teeth of pristiophorid sawsharks and pristid sawfishes and the dorsal spines of squalid and heterodontid sharks and chimaerids. When captured by gillnet or hook, fast swimming species, dependent on ram-jet ventilation of their gills for respiration tend to die more quickly than bottom-dwelling species when caught. Bottom-dwelling species with spiracles to aid gill ventilation are better able to pass water over their gills after capture by gillnets and can struggle vigorously to either escape or become more tightly enmeshed in the gear. Species that can struggle vigorously after capture in gillnets tend to have narrower selectivity ranges than species that struggle less. Hence, for some species, careful regulation of mesh-size can be used to ensure that the sharks captured are large enough to avoid growth overfishing and small enough to facilitate escapement of large breeding animals to avoid recruitment overfishing (Walker, 1998).

The concept of catchability is usually applied to target and byproduct species where most of the animals captured are retained. So as to broaden the concept to include bycatch, the term "catch susceptibility" (Stobutzki *et al.*, 2002) and the term "post-capture mortality" are adopted here to describe the survival of that part of the catch that is released. The parameters catch susceptibility and post-capture mortality both have values in the range 0–1 and are related to each other and to catchability by the equation:

$$\textit{catch susceptibility} = \textit{catchability} \times \textit{post-capture mortality}$$

which can hence be further expanded to provide the equation:

$$\textit{catch susceptibility} = \textit{availability} \times \textit{encounterability} \times \textit{selectivity} \times \textit{post-capture mortality}$$

Post-capture mortality is the proportion of fish that die as a result of being caught in, or encountering the fishing gear. Fish of target and byproduct species that are mostly retained have a post-capture mortality value approaching one. This can be less if some are discarded because of their size or breeding condition. Post-capture mortality for discarded species can vary markedly. In addition to handling by fishers, the fishing gear and biological characteristics can contribute to various kinds of mortality referred to as unaccounted fishing mortality or collateral mortality. Dead sharks not tightly enmeshed can drop out of gillnets and contribute to unaccounted fishing mortality through drop-out mortality. Sharks eaten by other fish or mammals after capture in the gear contribute to unaccounted fishing mortality through predation mortality. Dead sharks, either partly or totally decomposed or eaten by invertebrates and vertebrates when fishing gear is left in the water for extended periods, also contribute to unaccounted fishing mortality. Lost gillnets contribute to unaccounted fishing mortality through ghost fishing mortality until they are rolled into a ball by tidal flow. Postcapture mortality from normal handling by fishers is low for heterodontid and orectolobid sharks but high for carcharhinids.

13.2.4 Rapid assessment for evaluation of risk

Stock assessment of chondrichthyan species that incorporates time series of catch and indices of relative abundance, includes biological parameters and accounts for fishing gear selectivity has been undertaken for only a few species, such as *Mustelus antarcticus* (Walker, 1994; Walker, 1998) and *Galeorhinus galeus* harvested of southern Australia. The assessments of *G. galeus* also incorporate spatiality (Punt *et al.*, 2000) and evaluation of risk in a Bayesian framework (Punt *et al.*, 2000; Punt and Walker, 1998). Such assessments require large data sets from long-term fishery monitoring and extensive biological and gear selectivity studies (see Section 10). Because of their comparatively low biological productivity and, for many species, their high catch susceptibility, most chondrichthyan species require management action long before sufficient data are available to undertake a full stock assessment. It is therefore necessary to apply rapid assessment techniques for evaluation of risk from the effects of fishing.

A rapid assessment approach for evaluating risk to chondrichthyan species was applied to species caught as bycatch in a tropical prawn fishery in northern Australia (Stobutzki *et al.*, 2002). This method ranks the relative sustainability of each species on the basis of its "susceptibility" and "recovery" (Stobutzki, Miller and Brewer, 2001; Stobutzki *et al.*, 2002), which are assessed on the basis of the biological attributes of the species. A similar approach is proposed here for sharks and other chondrichthyans, but the approach alters the terminology and the method of quantification of the various parameters used to be more compatible with more comprehensive fishery assessment methods.

The method proposed here provides a framework for considering a species" ecological risk, risk of depletion or risk of extinction. For this method, the terms "catch susceptibility" and "biological productivity" are used in place of susceptibility and recovery to represent parameters associated with fishing mortality and population growth, respectively.

Species of high biological productivity can be viewed as having rapid population turnover, whereas species of low biological productivity can be viewed as having slow population turnover. For an unexploited population to remain in equilibrium, there has to be a balance between the natural mortality rate reducing numbers and the reproductive rate increasing numbers. Otherwise, over time, if the reproductive rate exceeded the natural mortality rate, the population would grow to infinity; conversely, if the natural mortality rate exceeded the reproductive rate, the population would go extinct. Low reproductive rate and low natural mortality rate are associated with low biological productivity, whereas high reproductive rate and high natural mortality rate are associated with high biological productivity. It follows, therefore, that either reproductive rate or natural mortality rate can serve as a proxy for biological productivity for rapid assessment.

Other expressions of biological productivity include the "intrinsic rate of population growth" parameter formulated variously in biomass dynamics models (Schaefer, 1957; Schnute, 1985), demographic models (Lotka, 1922) and various adaptations of these models for sharks (Au and Smith, 1997; Xiao and Walker, 2000). Using a particular formulation of a demographic model to allow for density-dependent change in natural mortality (Au and Smith, 1997), Smith, Au and Show (1998) classed 26 Pacific shark species on the basis of the "intrinsic rate of population growth" (referred to by the authors as "rebound potential") . In addition, intrinsic rate of population growth is related to inter-generation period and reproductive output per generation (Heron, 1972). Application of biomass dynamics models requires time series of catch and relative abundance data and demographic analysis combines available parameter estimates for natural mortality rate and reproduction. Required information on chondrichthyan reproduction for a population for this purpose includes the maternity ogive (proportion of the female population contributing to annual recruitment expressed as a function of length or age), fecundity expressed as a function of maternal length or age and sex ratio of progeny. If the maternity ogive and fecundity are expressed as a function of length, then the relationship between length and age is also required for the application of demographic models.

Using the natural mortality rate as a proxy for biological productivity requires some caution, as the natural mortality rate is likely to be density-dependent and age-dependent. Also, fishing is likely to remove the oldest animals from the population and reduce the maximum age detected in a sample of animals collected for ageing purposes. Notwithstanding these potential biases, rough estimates of natural mortality or maximum age can be used for broad categorization of risk. The instantaneous mortality rate, M, can be approximately related to maximum age, t_{max}, by the equation $\ln(0.01) = -M\ t_{max}$ where 0.01 represents survival of 1% of the animals reaching maximum age (Hoenig, 1983). Because natural mortality rate is much higher for the young age-classes than the older age-classes, as demonstrated from modelling shark populations (Punt and Walker, 1998; Walker, 1994), this equation is reformulated here for application to chondrichthyans by considering only that part of the population of age greater than 2 years. Assuming that mortality is constant for all age-classes, calculations of instantaneous total mortality rate of 1% for 2-year-old animals to survive to ages 8, 16 and 24 years are 0.77, 0.33 and 0.21, respectively. If total mortality is divided evenly between natural mortality and fishing mortality, a condition sometimes assumed for a population in equilibrium to produce the maximum sustainable yield (Au and Smith, 1997; Thompson, 1992), natural mortality rates for 2-year-old animals surviving to these ages approximate to 0.38, 0.16 and 0.10, respectively. These values are used as a basis for arbitrary categorization of chondrichthyan species risk (Table 13.1). For example, based on published instantaneous natural mortality rates, *Galeorhinus galeus* (Punt and Walker, 1998; Smith, Au and Show, 1998), *Carcharodon carcharias*, *Carcharias taurus*, *Carcharhinus plumbeus* and *C. obscurus* (Smith, Au and Show, 1998) can be classed at high risk. Similarly *Mustelus antarcticus* (Walker, 1994), *M. californicus*, *M. henlei* and *Sphyrna tiburo* (Smith, Au and Show, 1998) can be classed at medium risk and *Rhizoprionodon terraenovae* can be classed at low risk (Smith, Au and Show, 1998).

TABLE 13.1
Values of various parameters for three arbitraty categories of risk.

Parameter	Values for three arbitrary categories of risk		
	Low (L)	Medium (M)	High (H)
Total mortality (y^{-1})	>0.76	0.32–0.76	0.00–0.31
Natural mortality (y^{-1})	>0.38	0.16–0.38	0.00–0.15
Maximum age (y)	0–8	9–16	>16
Availability	0.00–0.33	0.34–0.66	0.67–1.00
Encounterability	0.00–0.33	0.34–0.66	0.67–1.00
Selectivity	0.00–0.33	0.34–0.66	0.67–1.00
Post-capture mortality	0.00–0.33	0.34–0.66	0.67–1.00
Catch susceptibility	0.00–0.33	0.34–0.66	0.67–1.00

Catch susceptibility and each of its four components (availability, encounterability, selectivity and post-capture mortality) can also be arbitrarily divided into three categories of risk. This is achieved here by evenly dividing the possible value range of 0.00–1.00 into the three ranges 0.00–0.33, 0.34– 0.66 and 0.67–1.00, designated low (L), medium (M) and high (H), respectively. For example, in each fishing method adopted in the fisheries of south-eastern Australia, it is possible to categorize encounterability, selectivity and post-capture mortality into one of the three categories on the basis of chondrichthyan taxonomic order (Table 13.2) by considering the animals" biological characteristics. This means that the only parameter to be determined for any particular species is "availability", which for rapid assessment can be estimated as the ratio of the area fished within the spatial range of that species divided by the entire area inhabited by the species. By adopting the upper limit values for the three ranges of 0.33, 0.66 and 1.00 for low, medium and high risk, respectively, then catch susceptibility can also be categorized as low, medium or high risk. For example for a fishing method where availability is low, encounterability is high, selectivity is high and post-capture mortality is high, then "catch susceptibility" is low. This is calculated as catch susceptibility = 0.33 x 1.00 x 1.00 x 1.00 = 0.33 (i.e. catch susceptibility = LHHH = L).

TABLE 13.2
Catch susceptibility of chondrichthyan animals to demersal fishing gear.

Catch susceptibility is defined as 'availability' x 'encounterability' x 'selectivity' x 'post-capture mortality'; 'availability' is the ratio of area of range of species divided by the area of the range of the fishery; 'catch susceptibility', 'availability', 'vulnerability', 'selectivity', and 'discard post-harvest mortality' all have values ranging 0–1, for risk assessment these are categorised as L (low, 0.00–0.33), M (medium, 0.34–0.66), and H (high, 0.67–1.00).

Taxonomic order	Common name	Encounterability				Selectivity				Discard post-harvest mortality			
		Trawl/ seine	Gillnet	Hook	Trap/pot	Trawl/ seine	Gillnet 6–6½ in	Hook	Trap/pot	Trawl/ seine	Gillnet 6–6½ in	Hook	Trap/pot
Pelagic and semipelagic species													
Carcharhiniformes	Whaler & hammerhead sharks	L	L	L	L	H	M	H	L	H	H	M	H
Lamniformes	Mackerel & thresher sharks	L	L	M	L	H	M	H	L	H	H	M	H
Demersal species													
Carcharhiniformes	Whaler & hammerhead sharks	L	H	H	L	H	M	H	L	H	M	L	H
Squatiniformes	Angel sharks	H	L	L	L	H	L	H	M	M	L	L	L
Pristiophoriformes	Sawsharks	M	H	M	L	H	H	H	M	H	H	L	M
Squaliformes	Dogfishes	M	H	H	L	H	L	H	H	M	M	L	L
Hexanchiformes	Sixgill & sevengill sharks	L	H	H	L	H	M	H	H	H	H	M	H
Orectolobiformes	Catsharks, wobbegongs, carpet	M	H	H	M	H	M	H	H	M	L	L	L
Heterodontiformes	Horn sharks	M	H	M	L	H	M	H	H	M	L	L	L
Pristiformes	Sawfishes	H	L	L	L	H	H	H	H	H	L	L	L
Rhinobatiformes	Shovelnose and guitar rays	H	L	L	L	H	L	H	H	H	L	L	L
Torpediniformes	Electric rays	H	L	L	L	H	L	H	H	H	L	L	L
Rajiformes	Skates	H	L	L	L	H	L	H	H	H	L	L	L
Myliobatiformes	Eagle & devil rays and stingrays	H	L	L	L	H	L	H	H	H	L	L	L
Holocephaliformes	Chimaeras	M	L	L	L	H	M	H	H	H	H	M	L

Footnote: The values presented in this table are based on species found in south-eastern Australia, but they should be applicable to most regions of the world, except 'selectivity' of gillnets presented here is for 6–6½ inch mesh-size which is likely to vary with region depending on size of animals for each species in the region.

13.3 FRAMEWORKS FOR FISHERIES MANAGEMENT

13.3.1 International developments

Growing widespread concern during the past decade about expanding fisheries for sharks and for the potential impacts of fishing on their populations and those of rays and chimaeras led to initiatives to implement better management of these animals. During the mid-1990s, submissions were presented to the Convention for International Trade in Endangered Species of Wild Fauna and Flora (CITES) seeking restrictions on the trade of products from sharks as a means of controlling the harvest of these animals. In response to requests from its members, the Food and Agricultural Organization of the United Nations (FAO) subsequently initiated a process that led to development of the International Plan of Action for the Conservation and Management of Sharks (IPOA-Sharks). The IPOA-Sharks was endorsed by the FAO Committee of Fisheries (COFI) during 15–19 February 1999. The IPOA-Sharks provides guidelines to member nations for development of National Plans of Action for the Conservation and Management of Sharks (NPOA-Sharks) and for coordination of shark management at global, regional and sub-regional levels under the auspices of FAO. The IPOA-Sharks supplements the Code of Conduct for Responsible Fisheries and defines "sharks" to include sharks, rays and chimaeras.

Through the IPOA-Sharks and other international developments, the scope of fisheries management for these animals is expanding beyond the focus of sustainable use of the resource to take account of the need for biodiversity conservation and maintenance of ecosystem structure and function. There is also growing emphasis on bycatch reduction and on ethical issues associated with full utilization of dead sharks and the handling and processing of these animals (FAO, 2000).

13.3.2 Jurisdictional and institutional frameworks

Fisheries management presupposes a minimum set of institutional arrangements and recurrent activities at local, sub-national, national, regional and global levels. Entities engaged in fisheries management require appropriate policy and legal and institutional frameworks to adopt measures for the long-term conservation and sustainable use of shark fishery resources. Conservation and management measures need to be based on the best scientific evidence available. Effective coordination of implementation of fisheries management at a national level through development of shark plans and ongoing shark assessments requires a structure, a definition of roles, agreed processes and mobilization of resources. All relevant fishing sectors, fishing communities, non-government organizations and other interested parties should be consulted as part of the decision-making process. Creation of public awareness of the need for the management of shark resources and participation in the management process by those affected should be promoted.

To be effective, management of fisheries has to be concerned with whole stock units over the entire area of distribution of the species harvested. The best scientific evidence available should be used to determine the area of distribution of the resource and the area through which a fish in the stock migrates during its life cycle. Where a stock falls entirely within the Exclusive Economic Zone (EEZ) of a single nation then that resource can be managed under the single jurisdiction of that nation. Where a stock straddles in the EEZs of more than one nation and, or, the high seas, complex jurisdictional arrangements are required. Shared or trans-boundary straddling-stocks need to be managed through bilateral and multilateral arrangements or Regional Fisheries Management Organizations (RFMOs) (FAO, 2000).

All nations are free to harvest fish in the high seas and regulation is beyond the control of any individual country. Straddling and highly migratory fish stocks maybe managed cooperatively the Agreement for the Implementation of the United Nations Convention on the Law of the Sea of 10 December 1982 Relating to the Convention and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, more briefly termed the UN Fish Stocks Agreement. Ratification of the Agreement by nations provides rights to, and obligations on those nations and prescribes fisheries management principles for the long-term conservation and sustainable use of straddling and highly migratory fish stocks. The Agreement provides a framework for cooperation between fishing nations, including through RFMOs. It also provides rights to member nations of RFMOs to board and inspect member fishing vessels on the high seas to check compliance with regionally agreed conservation and management measures. Nations signing the Agreement accept the principles of the Agreement. The UN Fish Stocks Agreement depends on "flag State responsibility", which is a principle of international law. The national law applying to a vessel on the high seas is the law of the country whose flag the vessel is entitled to carry. If there is any infringement of rules, the flag State of the vessel concerned is responsible for investigating and taking appropriate enforcement action.

13.4 USE RIGHTS

13.4.1 Benefits of use rights

Granting use rights bestows property rights whereby an individual, company, or defined group or community can own fish after the fish have been captured. Once captured the fish become private property. Before they are captured, the fish are private property only if the water body holding the fish is private property. Within a country's EEZ, fish in the water are usually deemed the property of the citizens of that country and said to be state property. Nevertheless, a state can legislate to privatize fish in the water for harvesting rights and thereby grant ownership to an individual, company, or defined group or community. Where the fish in the water are owned in common by a defined group or community, the fish are said to be their common property. For example, where a government legislates to bestow ownership of fish in a specific body of water to people traditionally using that fish resource, the fish in the water become the common property of those people. However, the fish of an entire nation are often referred to as common property. Here the group or community is defined as including all citizens of a nation; the term common property here maybe equated to state property (Charles, 2002).

Through fisheries management, use rights can be implemented under private property, state property or common property. In addition, the UN Fish Stocks Agreement (Article 10) provides a facility to prescribe use rights in waters outside the EEZs of nations on the high seas where the fish in the water are deemed "non-property" (Charles, 2002). Fishery managers need to ensure that no vessel is allowed to capture sharks or take sharks as bycatch unless authorized in a manner consistent with international law for the high seas or in conformity with national or sub-national legislation within areas of national or sub-national jurisdiction.

The FAO World Fisheries Conference in Rome during 1983 recognized that open access to non-managed fisheries resulted in competition for limited resources, overcapitalization of the industry and depletion of stocks. It was considered that fishers should have clearly-defined fishing rights and that catches should not exceed the productivity of the resource. One approach to allocate rights for the capacity to fish is through input controls such as licence allocation. Another approach is to allocate rights for specified shares of the resource through output controls in the form of catch quotas (King, 1995).

13.4.2 Territorial use rights

Rights can be assigned to individuals or communities to fish in certain locations based on longstanding tradition of use (customary usage). This approach is variously termed territorial use rights in fishing (TURFs) and customary marine tenure (CMT). A feature of these systems is the local solution of usage issues. Many fishing communities informally regulate their fishing effort, based on their observations of fish abundance and their interpretation of their indicators of abundance over time (Charles, 2002).

Territorial management is highly effective where it is supervised by the fishing community itself or by its elected leaders. Many TURF and CMT systems have declined as traditional fisheries commercialize. Nevertheless, several countries of Oceania, such as Solomon Islands, Fiji and Samoa, have moved to re-establish these systems. Customary fishing ground boundaries based on oral claims are being formalized in legislation (Charles, 2002). Japan, for example, has integrated ancient local systems of management into fisheries planning at all levels of local, regional and national government (Pinkerton, 2002). A challenge for countries is to support traditional approaches to management and to integrate them into regional and national management systems through co-management agreements. There is evidence of customary usage of sharks and rays in Canada, northern Australia (Last and Stevens, 1994), Solomon Islands (Sant and Hayes, 1996) and New Zealand (Francis, 1998). However, there are no examples where territorial use rights have been formally granted specifically for the harvest of chondrichthyan animals in recognition of traditional usage.

13.4.3 Limited entry

Limited entry is a common management tool whereby the management agency issues a limited number of licences to take fish. This creates a use right to participate in a particular fishery. Licence limitation is the restriction of fishing rights to those fishers, fishing units or fishing vessels licenced in a fishery.

Several types of fishing licences are used for fisheries management throughout the world. A "personal licence" authorizes a particular fisher to deploy fishing gear for catching fish, but requires the licenced fisher to be present at the site of fishing operations. A "vessel licence" authorizes a particular vessel to deploy fishing gear for catching fish, but requires operations to be made from the licenced vessel. A "fishery access licence" authorizes the holder, or a person nominated by the holder, to deploy fishing gear for catching fish from any nominated vessel. A "gear licence" authorizes the use of a particular item of fishing gear for catching fish by the holder, or a person nominated by the holder, from any nominated vessel. Special conditions or endorsements on such licences can be used to nominate one or more fisheries, species, gears, catch levels or effort levels that are authorized.

Licences are either non-transferable or transferable. Non-transferable licences are auctioned or issued at the discretion of the licensing authority through a Minister of State. Development of merit criteria as guidelines for issuing non-transferable licences by licensing authorities are usually criticized as discriminatory. Allocation of non-transferable licences according to merit inevitably leads to dissatisfaction and pressure from holders to make the licences transferable. Transferable licences are exchanged by mutual financial agreement between the seller and buyer, usually within guidelines prescribed by the licensing authority. Once transferable, licences acquire a value related to earnings that might be acquired from possessing the licence. Debts associated with the purchase of transferable licences create an incentive to increase the catch to service the loans, which create a need to reduce the number of licences or entitlements associated with each licence. If there is the need to reduce the number of licences in a fishery, the licensing authority can withhold non-transferable licences, but has to buy back transferable licences from licence holders at market price.

Annual licence fees collected by the licensing authority can be used to recoup management, surveillance, research and fishery monitoring costs and collect a resource rent on behalf of the community. Personal licences can be effective in artisanal and recreational fisheries, but fishery access or vessel licences are favored in industrial fisheries where costly assets are required and there is a need to exchange fishing masters or skippers on a vessel to ensure its economic viability. All four types of licence have been variously applied in fisheries either targeting sharks or taking sharks as byproduct or bycatch.

Limited entry caps the number of operators in a fishery, but is rarely sufficient to manage a fishery. Once licence limitation is implemented, improved skill of the operators and technological innovation inevitably increase the fishing power of the vessels in the fleet. Limited entry is best implemented during the early phase of the development of a fishery, before the catching power of the fleet is excessive. It is difficult to reduce the number of licences once there is over-capacity in the fleet. Whereas limited entry is a reasonable mechanism for assigning use rights, it must be implemented as part of a portfolio of management actions.

13.4.4 Quantitative input rights (effort rights)

Input controls designed to limit or reduce fishing mortality require some form of restrictive licensing, which limits the number of fishing vessels engaged in a particular fishery and some measure for limiting the fishing effort of the licenced vessels. Where over-fishing occurs and the fleet is too large, there is a need to reduce the number of licenced vessels or reduce the fishing efficiency of the vessels. Further, where licence limitation is established, incremental technological advances in vessel and fishing gear design and improvements in fish-finding equipment and navigation aids are likely to cause the effective fishing capacity of a fleet to increase with time. In addition, if the licences are transferable and acquire progressively higher value, economic forces will cause inactive vessels with their associated latent effort to become active and increase the total effort applied by the entire fleet. Hence, with any input control system, increasing efficiency and increasing effort create an ongoing need to reduce the number of vessels or efficiency of each vessel. Over-capacity of a fleet can be reduced in several ways: removing vessels, reducing fishing time of the vessels, limiting the amount or size of gear that a vessel can carry, or reducing efficiency of fishing effort.

Removing vessels from the fleet requires rescinding licences. This involves removing the rights from some vessels to operate in a fleet. One system applied for this purpose is referred to as a Buy-Back Scheme or Decommissioning Scheme where funds are made available by government, the industry itself or some other stakeholder group to purchase licences as a means to removing vessels from the fishery. A feature with these schemes is that the least efficient operators have the highest economic incentive to sell their licences. Whereas this improves the overall economic efficiency of the fleet, it can result in a large number of vessels being removed with little change in overall fishing mortality.

Reducing vessels" fishing time can be implemented by imposing limits on the number of days or times of the day vessels can operate. Extended closed seasons, closed days of the week, or closed times of day are unpopular with fishers as it reduces flexibility and creates incentives to operate under adverse weather conditions. Closed days of the week are seen as inequitable as it effects greatest on larger vessels that undertake extended periods at sea. Closed periods disrupt market supply of fish and employment patterns.

Fishing capacity of a fleet can be restricted by limiting the size of vessel and engine power and thereby restrict the ability of vessels to tow fishing gear such as demersal trawls. For most other fishing methods, however, the relationship between the size of the gear and the size of the vessel or power of the engine is not so clear. Nevertheless, fishing capacity of a fleet can be restricted by limiting the size of vessels and thereby restricting the number of fishing days by weather conditions. This can cause problems of safety for fishers if there are strong economic incentives to operate under hazardous conditions.

Fishing gear can be limited in type, size and number. Gillnets can be restricted by controlling the length and height of the nets, the mesh-size of the webbing and hanging ratio for the construction of the nets. Longlines can be restricted by controlling the length (or volume) of mainline and the number of hooks that can be used during each operation. Restrictions can also be placed on hook size and presence or absence of a wire trace between the hook and the snood and on the use of automatic baiting and setting machines. Trawl nets can be limited to a maximum length of headline.

Gear regulations tend to restrict the efficiency and cost of catching fish for each operator. Gear restrictions are often implemented where there are the social objectives of providing employment and food to a large number of traditional and artisan fishers. Hence, gear restrictions are minimized where there is the economic management goal for reducing the number of operators and improving economic efficiency, but can be adopted as a means to maintain fishing communities and promote equity of incomes among participants (Pope, 2002).

Some of the benefits of limits on the quantity of fixed gear used, such as gillnets, can be offset by the gear being in the water for extended periods. Legislating for vessels not to leave the gear unattended discourages the practice of returning to port while the gear remains set at sea. This practice leads to cryptic fishing mortality from predation mortality and ghost fishing mortality if the nets are lost.

Meeting the biological objective of reducing fishing mortality by reducing vessel efficiency is incompatible with the economic objective of improving economic efficiency of the fleet. Similarly, meeting the biological objective by reducing vessel numbers is incompatible with the social objective of providing employment for fishing communities.

There are many general vessel and fishing regulations that apply across fisheries, but few have been implemented specifically for chondrichthyan species. Within the European Union, every country has agreed to a maximum gross tonnage of vessels and maximum engine power. The limits are set for each fishery, fishery sector and, in some cases, fish stock (Pawson and Vince, 1999).

During the late 1980s and the 1990s, a complex system of quantitative rights was adopted for the shark fishery of southern Australia. Depending on historic catches by a vessel, vessel licences were endorsed to use various length of gillnets. These gear holdings were not transferable except for a short period when a small proportion of the licences could be amalgamated to allow for an increase in gear holdings. After amalgamation, the maximum gear holding was 6000 meters long, but this was subsequently reduced to 4200 meters (Walker, 1999). This type of effort rights was taken a step further in the shark fishery of Western Australia. Here time-gear units were allocated where a time-gear unit authorized the use of a particular length of gillnet for one month of the year (Simpfendorfer, 1999).

13.4.5 Quantitative output rights (catch quotas)

Limitation of catch, also referred to as output control, can take the form of a global catch quota, individual quotas as non-transferable individual quotas or individual transferable quotas (ITQs) with a total allowable catch (TAC), bag limits or trip limits.

A global catch quota, commonly referred to as a competitive TAC, is the maximum catch allowed from a resource by the entire fleet for a year or season. Under this system, individual fishers compete for catch until the fleet reaches the overall limit and the fishery is then closed. Such a system requires rapid collation of catch statistics to be effective. Individual fishers feel compelled to operate under hazardous weather conditions and to invest in vessel capacity and gear to attain a competitive edge. This can result in progressively shorter seasons, which disrupt employment patterns and market supplies.

Bag limits are a simpler form of regulation where the number of animals a person or vessel can retain is limited. Bag limits are usually applied on a daily basis for recreational fishers where an individual is permitted to land up to a specified catch weight or a prescribed number of carcasses. Limiting the number of carcasses can create an incentive to retain the largest animals and discard small animals, which might be dead and hence contribute to cryptic fishing mortality.

Trip limits may be applied on a trip or daily basis for fishers who do not hold a licence to operate in the fishery. Trip limits may be designed to avoid wastage by allowing non-licenced operators to land byproduct catch. However, the trip limit needs to be sufficiently low so as not to encourage targeting by non-licenced operators. Trip limits may be also applied in a fishery to discourage "derby fishing" and to spread the take of a quota over a long period of time.

Individual non-transferable quotas are are prescribed for each operator's catch, which is usually fixed as a specified proportion of the TAC. This avoids the competitive element, but does not allow an operator to increase catch by personal choice.

Individual Transferable Quotas (ITQs) provide each operator with a prescribed catch of one or more units of catch. The ITQs can be traded freely, or traded between specified operators. Operators can hold one or more ITQs, depending on the number they choose to buy. By prescribing an ITQ or non-transferable quota as a proportion of the TAC, the catch allowed under each ITQ varies depending on the TAC, which can be set annually or for some other period. The facility to trade ITQs allows less efficient operators to sell all or part of their quota to more efficient operators at the market price of the quota. A substantial enforcement effort is required to ensure that individual quotas are not exceeded. Individual catch quotas create an incentive to under-report catches and a temptation to sell illegal catch to black market buyers.

In addition, management by individual quotas can encourage operators to discard that part of the catch that potentially receives a low price (e.g. damaged, small or large animals) and replace them with animals that would receive a higher price, a practice referred to as high grading.

TACs for some species of fish are expressed as the number of fish, but they are usually expressed in terms of weight. Although they should ideally relate to the catch, for administrative convenience they are limits on landings. Components of TACs are often used as a basis for resource allocation between different user groups, such as between recreational users and commercial users or between sectors or regions of the commercial users. This also occurs in internationally shared fisheries where allocations are negotiated between countries.

Various types of TACs are administered for shark resources. For management of the United States Atlantic Shark Fishery, 39 species of sharks are categorized into four groups: "large coastal", "small coastal", "pelagic" and "prohibited" for the commercial sectors of the fishery. Apart from the prohibited group, each group has a separate TAC, reviewed periodically. In the absence of limited entry in the fishery, the commercial catches have regularly exceeded the TACs. In addition, there is a commercial trip limit of 4000 pounds for the large coastal group and a recreational fishing bag limit of two sharks per boat per day plus two Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) per person per day or trip (Branstetter, 1999). New Zealand and Australia have set TACs for individual species of shark and have an ITQ system of management (Francis, 1998; Walker, 1999).

13.5 TECHNICAL MEASURES

13.5.1 Regulation of fishing gear

Ideal fishing gear achieves many things simultaneously. It is efficient at capturing target species while avoiding small fishes so as to minimize growth overfishing and avoiding large breeding animals to minimize recruitment overfishing of the species. It has negligible direct or indirect impact on bycatch species, habitats and substrates and it causes minimal damage to animals captured and in no way diminishes the food quality of the animals caught.

Regulation of fishing gear can be used to control fishing mortality, impacts on habitats and ecosystems and food quality of fish retained. Regulation of fishing gear should not be used as a way of controlling the fishing effort component of fishing mortality, but rather as a way of controlling the catch susceptibility component of fishing mortality. This can be achieved by variously controlling one or more of the four components of catch susceptibility – availability, encounterability, selectivity and post-capture mortality. Availability can be controlled through fishing area closures to the use of specific gears, whereas encounterability, selectivity and post-capture mortality can be controlled or regulated through the manner of gear construction or the way it is used.

Fishing gears maybe classified as passive or active. This classification is based on the behaviour of the target species in relation to the gear. Passive gears include gillnets, trammel nets, longlines, handlines, jigs, droplines, troll lines, pots and fish traps. Active gears include spears, harpoons, dredges, demersal trawls, mid-water trawls, Danish seine nets, Scottish seine nets, beach seines and purse seines. Table 13.3 provides an evaluation of different fishing gears for selectivity and ecosystem effects of fishing. The values presented are from evaluation across many fisheries, but specific values for a particular fishery, particularly as it might relate to chondrichthyan species, can be altered depending on regulation of the fishing gear (Bjordal, 2002).

TABLE 13.3

Estimates of ecosystem effects of fishing for different fishing gears.

Ranking is a scale from 1 (non favourable) to 10 (highly favourable) for different ecosystem related factors. The ecosystem effect index is the mean of the other seven factors (reproduced from (Bjordal, 2002).

Fishing gear	Size selection	Species selection	Bycatch mortality	Ghost fishing	Habitat effects	Energy efficiency	Catch quality	Ecosystem effect index
Gillnets	8	4	5	1	7	8	5	5.4
Trammel nets	2	3	5	3	7	8	5	4.7
Handlining	4	4	6	10	9	9	9	7.3
Longlining	6	5	6	9	8	8	8	7.1
Pots	7	7	9	3	8	8	9	7.3
Traps	5	5	8	8	9	9	9	7.6
Spear, harpoon	8	9	5	10	10	8	9	8.4
Pelagic trawl	4	7	3	9	9	4	8	6.3
Demersal trawl	4	4	6	9	2	2	6	4.7
Beam trawl	4	4	6	9	2	1	6	4.6
Shrimp trawl	1	1	7	9	4	2	6	4.3
Seine net	5	5	6	9	4	5	8	6.0
Purse seine	-	7	5	9	9	8	8	7.7
Beach seine	2	2	5	9	6	9	9	6.1

Fishery managers need to ensure that fishing methods and practices in a fishery are consistent with the FAO Code of Conduct for Responsible Fisheries. Those methods that are not should be phased out and replaced with acceptable methods and practices (FAO, 1995, 2000).

The type of fishing gear used and the species of shark taken as bycatch determines which techniques and equipment are appropriate for minimizing bycatch. For trawl nets, there is evidence that catches of sharks have been reduced when fitted with turtle exclusion devices, suggesting there might be advantages investigating alternative devices designed specifically to exclude sharks. Also, there is scope to reduce bycatch of sharks in gillnets by regulating mesh-size and possibly the breaking strain of the webbing filaments. Many species of sharks remain alive on hooks for extended periods and can be released alive. There might be scope to improve survival of sharks by prohibiting the use of wire traces used to attach hooks to the snoods on a longline and by regulating for reduced breaking strains of the snoods. Wire traces reduce the probability of hooks being bitten off the snoods by sharks. Regulation of hook size may provide a means of eliminating or reducing the catch of smaller, younger individuals in a shark populations (Dowd, 2003, Musick, unpublished). Minimum mesh-sizes or square mesh panels in codends of trawl nets are widely applied, but are not intended specifically for chondrichthyan species. Selection of appropriate trawl codend mesh size and shape might have some benefit in allowing neonate and small juvenile sharks to escape.

Regulation of mesh-size is a highly effective measure for shark management. Careful selection of mid-sized mesh allows small animals to pass through the meshes and large animals, notably breeding and other mature animals, to escape (Kirkwood and Walker, 1986). Adoption of a predominantly 6-inch mesh-size during 1975 has been the key to success in sustainable use of the gummy shark (*Mustelus antarcticus*) stocks in Bass Strait. In this fishery, not only does the gear selectivity allow escapement of small and large animals, but the fishers operate in areas inhabited by mid-sized animals, which tend to be away from the inshore areas inhabited by pre-recruits and breeding females (Walker, 1998). In Western Australia, mesh sizes, vertical number of meshes and net length in the construction of shark gillnets are also controlled. These vary between different zones (Simpfendorfer, 1999).

13.5.2 Area and time restrictions

13.5.2.1 Protecting areas

Fishing closures involve restricting some or all methods of fishing in selected areas. Closures can be permanent, temporary, seasonal, daily or part of the day. Spatial and temporal closures are frequently applied to meet specific fishery-management objectives, but they are also used to meet other community objectives. Other objectives for closures include protecting marine, estuarine and freshwater biota, items of special cultural value, or geologic interest. In addition, areas might be set aside for specific purposes such as navigation, aquaculture or mining. The various purposes of closures have produced confusion and debate over terminology. For the purpose of this chapter, a distinction is made between closures designed to meet fisheries management objectives and closures designed to meet other community objectives. The two terms adopted are "fishing area closure" and "marine protected area".

These terms are not meant to be mutually exclusive, but rather to provide a means for distinguishing between addressing fisheries management objectives as they relate to sustainable use, biodiversity conservation and protection of ecosystem structure and function from the effects of fishing and addressing other community objectives. The fishery manager needs the flexibility of prescribing management boundaries and varying rules between zones. At the simplest level, this might be prohibiting angling from a jetty to avoid injury to bathers. At a more complex level action might zone a region of thousands of square kilometers to meet a range of fishery and ecological objectives through a system of licensing use rights, gear restrictions and area closures across several fisheries. For example, gear restrictions across a complex of zones might be designed to provide high sustainable yields from target species of high biological productivity, while simultaneously minimizing impacts on bycatch species of low biological productivity. Where marine protected areas are proposed within broad fishing areas, an astute fishery manager will endeavor to influence the positioning of the boundaries that are compatible with fisheries objectives or at least gain some benefit for a fishery. Examples of how marine protected areas and fishing area closures can benefit sustainable use of target species and biodiversity conservation of chondrichthyan animals are presented in the following section.

13.5.2.2 Marine protected area

A marine protected area (MPA) is defined by the World Conservation Union (IUCN) as "any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment" (Anon., 1988). An MPA can be large or small and the overall objectives for an MPA can be specific or broad. Large MPAs with broad objectives are often divided into geographically smaller zones. Depending upon the objectives, an MPA, or a zone within an MPA, might be designated for one or more uses. MPAs are usually defined based on judgement using qualitative information, as obtaining quantitative evaluation is costly and long time-series of environmental or community monitoring-data are rarely available. Selected areas are usually judged as being unique or having high conservation value. An example of a unique area declared as an MPA is the stromatolite assemblage of Shark Bay, Western Australia. Corner Inlet in Victoria, Australia, on the other hand, was declared an MPA in 1983 because it was judged to have several high conservation values. These values include the presence of international migratory birds, soft substrate biotic communities, mangrove stands and *Posidonia* sea grass meadows (Plummer *et al.*, 2003). In Australia and South Africa, for example, networks of MPAs are being established to protect representative areas of a range of habitat types.

MPAs with single or multiple zones have been declared throughout the world for providing various levels of protection and for a variety of uses. A preservation zone or wilderness zone usually provides the highest level of protection through very limited access. A cultural zone is designed to provide protection to special items of cultural value and sites of historic, cultural or religious significance. These include shipwrecks, archaeological relics, submerged aboriginal middens and fossils. Zones that allow for access, but with minimal disturbance, include educational, scientific, experimental and recreation zones. An educational zone is usually a relatively safe diving or intertidal area that can be visited for training and educational purposes. In scientific zones authorized researchers can undertake the study of particular species or ecology of marine communities. Other types of zones, such as recreational or traditional fishing zones, allow for exploitative activities. A recreational zone might allow for diving and photography but no fishing, or might allow for recreational fishing activities. A traditional fishing zone recognizes traditional fishing rights of a community or group of individuals and allows for ongoing subsistence fishing.

MPAs are highly suitable for management of chondrichthyan species that aggregate where they are vulnerable to capture or disturbance by human activities (Bonifil, 1999). There are several examples from various parts of the world where these have been applied for sharks and rays. In New South Wales, Australia, the grey nurse shark (Carcharias taurus) is fully protected, but, to avoid unintentional kill in the coastal waters from longline fishing, a system of 10 sanctuary areas was established in December 2002. Each sanctuary extends 200 metres out from an island or a section of coast with buffer zones extending a further 800 metres. Fishing is prohibited and new controls on scuba diving include bans on night diving, feeding, touching, harassing or chasing sharks and on use of electronic shark repelling devices and electric scooters in these areas. In the Florida Keys National Marine Sanctuary, nurse shark (Ginglymostoma cirratum) mating aggregations at the Dry Tortuga Island group were recently given added protection by implementing a seasonal closure to boat traffic (Bonfil, 1999; Stevens 2002). The Ningaloo Reef Marine Park in northern Western Australia on the edge of the Indian Ocean provides protection to whale shark (Rhincodon typus) when these animals aggregate in this region from late March to early May. The number of divers and hours that divers and boats can approach these animals is restricted. Touching the animals or use of camera-flash lights is prohibited (Tricas et al., 1997). The Kinabatangan wildlife sanctuary in Sabah, East Malaysia includes about 27 000 hectares of tropical forest and the lower reaches of the Kinabatangan River and provides some protection (although some artisanal fishers operate there) to several rare freshwater elasmobranch species. These include the river speartooth shark (Glyphis sp.), giant freshwater stingray (Himantura chaophraya) and greattooth sawfish (Pristis microdon) (Payne and Andau, 2002).

13.5.2.3 Fishing area closure

Fishing area closure is defined here as closing an area to all, or selected fishing gears for continuous or selected time periods to limit fishing mortality on all or particular length or age-classes of one or more fish species, or to reduce gear impacts on habitats or other uses. Fishing area closures can be applied to target, byproduct, or bycatch species. MPAs can also limit fishing mortality, but areas closed to meet fisheries management objectives are not normally referred to as MPAs, marine parks, reserves or sanctuaries. In MPAs, more than fishing mortality and impact of fishing gear are controlled.

Fishing area closures can be used as a fisheries management tool to meet specific fisheries objectives. One important objective is to protect aggregations of small (pre-recruit) animals to allow them to grow and thereby improve yield per recruit by avoiding growth over-fishing. Another important objective is to protect aggregations of breeding or mature animals to enhance survival of the largest animals and so produce the highest number of offspring and thereby avoid recruitment overfishing.

Fishing area closures will be used much more extensively in the future and there are several reasons why they have been applied conservatively in the past. First, fisheries managers have tended to focus attention on abundant species with high biological productivity, whereas closures are better for managing less abundant species with low biological productivity. Second, setting boundaries for closures requires extensive data sets to provide detailed information on distribution and biological condition of fish and often these data sets have not been available. Third, fishery managers have been reluctant to prescribe in law complex demarcation boundaries because they have been difficult to enforce and fishers have been often uncertain of their navigational position at sea in relation to demarcation boundaries.

There have been several developments in recent years to facilitate greater application of fishing area closures in the future. One of these developments is the growing awareness in the community that chondrichthyan species are among the least biologically productive animals and need special conservation and management attention. In addition, three important technological developments in recent years make fishing area closures a more practicable fisheries management tool. The first development is that of Geoglobal Positioning Systems (GPS), which enable the position of a vessel to be known continuously with high precision. The second development is that of Geographic Information Systems, which allow for better management, analysis and visual display of spatial data. This innovation provides a facility to better understand the spatial and temporal distributions of species and habitats and to better evaluate the significance of various areas. The third development is that of vessel monitoring systems (VMS), which overcome the need for deployment of high-cost patrol vessels. VMS allows the navigational positions of vessels at sea to be electronically monitored using satellite communication systems. As costs of VMS decline so too will the surveillance cost for effective enforcement of fishing area closures.

Two types of fishing area closures have been implemented in the shark fishery of southern Australia since the 1950s. Closure to shark longline fishing in nursery areas of school shark (*Galeorhinus galeus*) in the inshore waters of northern and south-eastern Tasmania were first adopted in 1954 and extended in the 1960s. In 1990, regulations were extended to included gillnets used for targeting sharks (>150 mm mesh-size) and gillnets for recreational and commercial fishing to target other species (60–70 mm mesh-size) in some of these areas. These closures were designed to prevent targeting pregnant females entering shallow waters for parturition, as well as to reduce the incidental kill of neonate and small juvenile animals (Williams and Schaap 1992). In addition, closed seasons during October or November (the months immediately prior to parturition) were adopted across the entire fishery during 1953–67. During 1994, the use of gillnets were prohibited during the period from 8 October to 22 November for the area west of the South Australia– Victoria border and during the period from 11 November to 25 December for the area east of the border. These rolling closures were designed to protect pregnant animals as they migrated from the western region of the fishery to the nursery areas in the eastern region for parturition (Walker, 1999).

Another example of a fishing area closure for sharks were the large areas closed to gillnet and longline fishing for sharks in Western Australia to protect breeding *Carcharhinus obscurus* and *C. plumbeus* (Simpfendorfer, 1999). Also, although not specifically designed for chondrichthyan species, many nations designate coastal waters for artisanal fisheries and those further offshore for industrial fleets. Though designed for social reasons, it does provide some limitation on fishing mortality in coastal waters.

The most promising approach to fisheries management is to take a more regional approach and adopt greater use of fishing area closures. There are numerous examples where fishing area closures have been applied in the past, but they have tended to be small inshore areas.

13.5.2.4 Regional fisheries management

Regional fisheries management is defined here as integrated management of a broad region of waters across species and fisheries. Management is through allocation of use rights and application of fishing area closures and other technical measures. It is designed to efficiently harvest resources in specified areas and to meet the triple goals of sustainable use with high yields, biodiversity conservation and maintenance of ecosystem resilience. Open and closed areas are selected to minimize impacts on pre-recruit and breeding and other mature animals of target species, on species of low biological productivity and on habitats, particularly critical habitats.

A regional approach to fisheries management through the judicial use of fishing area closures is required to avoid depletion of species with low biological productivity that are affected by fishing gear used to target species of high biological productivity. Maximum benefits from fishing area closures can be attained by aligning refuge areas for species of high catch susceptibility and low biological productivity (low reproductive rates and low natural mortality rates) with areas containing critical habitats and pre-recruit and breeding animals of the target species. While some trade-offs are inevitable, where practicable, the fishing area closures should not be so large that there are insufficient fishing grounds open to efficiently harvest high-valued target species to ensure high sustainable yields.

Regional fisheries management requires an exhaustive information base. Extensive data sets on monitoring distribution, abundance and fishing mortality and on critical habitats and population biology are not only required for intensive management of target species, but for all byproduct and bycatch species. The positions of the boundaries of the fishing area closures need to be flexible so they can be updated as improved information is acquired. Through improved information and an adaptive management approach, the goal is to optimize yields across species, biodiversity conservation and ecosystem maintenance.

The low biological productivity of many chondrichthyan species is likely to have a major influence on the boundaries of area closures and will provide an impetus to adopt the regional fisheries management approach. Also, species found in temperate regions tend to have lower productivity than those found in tropical regions and those found in cold deepwater on the continental slope tend to have lower biological productivity than those found in the warmer waters on the continental shelf in temperate regions. The recent depletion of the deepwater squalids and chimaerids on the continental slopes of the Earth's temperate regions, such as southern Australia (Graham, Andrew and Hodgson, 2001), has created a need to establish substantial refuge areas for these species.

Multispecies modelling tools for evaluation of alternative spatial policy options are emerging. Such models need to account for trophic interactions with important top-down impacts of predators on prey and dispersal responses of harvested species and redistribution of fishing effort in response to trophic cascades. Determination of appropriate sizes and effectiveness of closed areas are highly dependent on predator-prey relationships and movement rates of harvested species. In general, a few large closed fishing areas are likely to be more effective than a large number of small ones. Local protection can be negated by fishing effort concentrated at the boundaries of closed fishing areas or at nearby sites where the presence of prey species attracts mobile predator species from the closed areas (Walters, Pauly and Chistensen, 1999). Importantly, the perimeter-to-area ratio decreases as size of closed area increases. Closed area boundaries can be minimized by having large closed fishing areas and by placing the closed fishing areas adjacent to land or in bays and inlets (Walters, 2000).

Closure of fishing areas can have unintended consequences caused by the redistribution of effort from those areas, particularly if the fisheries are principally managed by TACs and ITQs. Whereas TACs and ITQs control the catch of quota species, which are usually target or byproduct species, they do not control bycatch species. Hence, redistributed effort from closed areas might have undesirable effects on bycatch species. A management alternative to TACs with ITQs is to adopt a total allowable effort with ITQs specified as "transferable effort quotas" (Walters and Bonfil 1999). These quotas could be allocated according to a carefully prescribed distributional pattern and would depend on VMS for control.

13.5.3 Product form

Products from sharks and other chondrichthyans, when landed, or later occur in many forms including whole animal, carcass, tissue or processed product. The carcass can be beheaded and eviscerated with skin on and fins on, beheaded and eviscerated with skin on and fins off, or beheaded and eviscerated with skin off and fins off. Tissues, body parts or product can be in the form of meat fillets, heads, jaws, head cartilage, vertebral column, powdered cartilage, skin, fins, whole livers, or liver oil.

This wide range of product forms creates difficulties identifying the species or measuring these animals when they are brought ashore. This results in ambiguity in the official catch statistics. Monitoring sex composition of the catch is not possible if the pelvic fines and claspers of males are removed. Monitoring length-frequency composition and enforcing size limits usually involves measuring partial length, which can be uncertain if all fins and the tail are removed.

Fishers should not be forced to land sharks whole, because sharks need to be gutted and gilled as soon as practicable after capture to avoid degrading the quality of the meat and other products. Species, sex and partial length of a shark can be determined ashore if sharks are beheaded and eviscerated at sea and landed in the product form as carcasses with fins, skin, claspers and, where applicable, dorsal spines attached. Leaving the head attached, with the gills removed, is an option where species identification from the carcass with fins attached is uncertain. If there is a requirement for species identification for marketing or trade purposes, field guides based on fins and other body parts will need to be prepared. There may also be advantages in establishing regulations to ensure that shark products (carcasses, meat, fins, skins, heads, vertebral columns, livers, liver oil and jaws) are clearly labelled with species name. If sharks are not required by law to be landed in a standard product form, statistics forms may require provision for reporting the product form of the sharks, in addition to reporting weight of catch. This also applies to data from landing sites, processing plants and markets and applies to trade data. All trade products should be specified by species and as frozen or dried. Without these provisions catch weights will be ambiguous.

If more than one product form occurs it is necessary to have appropriate weight conversion factors to produce a single set of standard statistics. Similarly, if it is necessary to adopt more than one standard length measurement, the data should be converted to a single standardized length, ideally total length or fork length.

To standardize the statistics for chondrichthyan species, Australia has adopted the following wording in its National Plan of Action for the Conservation and Management of Sharks (Anon., 2002).

- Fishers should be required to report shark weights for the form in which they are landed and, where practical, all sharks be landed in the carcass form where a carcass is defined as a beheaded and gutted shark with all fins and, for males, the claspers attached. Leaving the claspers intact enables monitoring the sex of sharks after landing ashore.
- Fishers should be required to report chimaera weights for the form in which they are landed. Where practical, all chimaeras should be landed in the carcass form where a carcass is defined as a beheaded and gutted chimaera with all fins and, for males, the claspers attached, except for the pectoral fins and belly flaps which are removed.

- The issue of standard reporting of rays needs to be addressed. There is a growing practice of retaining the outer margins of the discs (pectoral fins) of the animal and discarding the rest of the animal for several large-sized species. This involves retaining a relatively small proportion of the animal and might be regarded as wasteful and analogous to finning.
- Official statistics of catch weights should be published as standard carcass weights and, where reported by fishers in a different form, the weights are to be converted to the standard carcass form.

13.5.4 Size limits

Legal size limits can be minimum or maximum sizes. They can be an effective management measure where the animals are landed from the fishing gear live and in a condition where the survival rate of released animals is high. Conversely, size limits are ineffective where the animals are landed dead or in poor condition and survival of released animals is unlikely. Hence, they are effective for many species that survive release from hooks, seine nets and fish traps, but are ineffective for species released after capture where survival rates are low.

Legal minimum sizes can be used to avoid growth overfishing, which results in the yield from a fishery is sub-optimal as many of the fish are caught when they are small and the yield from the fishery is lower than the potential yield had the animals been given time to grow and increase their size.

Legal maximum sizes can be used to avoid recruitment overfishing. This maybe useful for those species of sharks where the proportion of the females in breeding condition each year increases with size and fecundity increases with maternal size. Where reproductive rates increase with size, the contribution to recruitment is likely to be much higher for large animals than for small animals. Hence, there can be stock benefits in releasing large animals live. A legal maximum size is likely to be of higher value for females than for males.

Further, there is usually a strong correlation between mercury concentration in shark meat and shark size (Forrester, Ketchen and Wong, 1972; Walker, 1976). Where the concentration in large animals exceeds food standards, the legal maximum sizes have occasionally been used as a means of reducing the number of sharks with high mercury concentrations from reaching the consumer (Walker, 1980).

Fishers recognize the benefit of releasing undersized animals and usually endorse legal minimum sizes as they understand that sharks can be recaptured at a later and larger size. On the other hand, they are less likely to support legal maximum sizes. Large animals have a higher market value and fishers are aware of the uncertainty of survival of large released animals. It is therefore preferable to apply alternative management measures to protect large animals.

Minimum and maximum legal sizes are usually expressed in terms of length. Because most sharks are beheaded when the animals are landed, length needs to be prescribed as a partial length rather than a total length. The longest reliable partial length that can be taken from a beheaded and eviscerated carcass is from the last gill-slit to the distal end of the caudal fin. The last gill-slit closely coincides with the anterior edge of the pectoral fin, or, where the fins are removed, the cartilage from the pectoral girdle is usually intact. Where the caudal fin is removed, then the base of the caudal fin should be used.

In Australia, a legal maximum length was applied for school shark (*Galeorhinus galeus*) in Victoria, during 1972–85 to reduce the average mercury concentration in shark meat reaching the consumer (Walker, 1999). For a similar reason, a maximum weight of 18 kg for a trimmed carcass applies to all sharks landed in Western Australia (Simpfendorfer, 1999). Legal minimum lengths for sharks have been applied in south-eastern Australia for school shark and gummy shark since 1949 (Walker, 1999).

13.6 SPECIAL PROTECTION OF THREATENED SPECIES

Naturally rare species and species with poor conservation status may require special protection or management through such measures as a prohibition on catch, injury or interference. When this happens accidentally, consideration should be given to establishing sanctuaries through fishing area closures or MPAs.

There are no internationally agreed definitions of "threatened" or "endangered with extinction," but some countries have adopted classifications such as "endangered," "threatened" and "depleted", which have legal status in their jurisdictions. The most widely accepted classification for the conservation status of chondrichthyan species is the IUCN Red List, which classifies species as "critically endangered", "endangered", "vulnerable", lower risk" and "data deficient". The first three of these are grouped as "threatened" species. Criteria for classifying species include rate of population depletion (percentage decline over three generations), overall population size and geographic area and extent of fragmentation within the distributional range of the species (Anon., 1994; Hilton-Taylor, 2000). Chondrichthyan species first appeared on the IUCN Red List in 1996 (Hudson and Mace, 1996). In 2000 when the list was last updated by the IUCN Shark Specialist Group, 40 chondrichthyan species were listed as threatened world-wide and an additional 5 species were listed within isolated local populations. More recently, 31 chondrichthyan species have been identified as becoming extinct at particular localities and one regionally extinct (Dulvy, Sadovy and Reynolds, 2003).

Some species are classed as threatened on the basis of extreme rarity. These include all river sharks (*Glyphis* spp.), all freshwater sawfish (*Pristis* spp.) and several other freshwater batoids. Others species are classified as threatened because their populations have been depleted by the effects of fishing. These include several species of angel shark (*Squatina* spp.) and batoid species severely impacted by trawl fisheries. Species, which have naturally small populations and have been depleted, include the whale shark (*Rhincodon typus*), basking shark (*Cetorhinus maximus*), grey nurse shark (*Carcharias taurus*) and white shark (*Carcharodon carcharias*) (Anon., in press; Camhi *et al.*, 1998).

Various initiatives to protect endangered species have been taken in various parts of the world. Fishing for whale sharks is banned in the Maldives. The number of divers and hours that divers and boats can approach these animals is restricted in Ningaloo Reef Marine Park to minimize disturbance. White shark is now protected in South Africa, Mamibia, Australia, USA, Maldives and Malta. In addition to declaring full protection for this species, Australia has developed species recovery plans for the white shark and grey nurse shark. Several additional steps have been taken to reduce the accidental kill, injury or disturbance of these animals. Ten grey nurse shark sanctuaries were recently declared in New South Wales waters and there is a total ban on the use of shark fishing gear and the use of mammal blood or oils for attracting sharks in all Victorian waters. There are legislative requirements to report all interactions with white sharks and codes of practice are being developed for eco-tourist activities.

13.7 PRODUCT CERTIFICATION AND ECOLABELLING

Product certification and ecolabelling can be applied in support of fisheries management. Product certification is a measure mandated by governments to ensure that only legally harvested and reported fish landings can be traded and sold on domestic and international markets. Product certification is an extension to normal fisheries management activities. Where there are problems regulating access, such as on the high seas, product certification schemes provide a means of reducing illegal, unreported and unregulated fishing. Ecolabelling programs can create market-based incentives for better management of fisheries by creating consumer demand for seafood products from well-managed stocks by tapping the growing public demand for environmentally preferable products. Criteria used for the accreditation process are a compromise between the demands of consumers and the capabilities and willingness of the producers to meet those demands (Wessells *et al.*, 2001).

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