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INSTITUTE

**DEVELOPMENT OF AN INTEGRATED FISHERIES
MANAGEMENT MODEL FOR KING GEORGE
WHITING (*SILLAGINODES PUNCTATA*)
IN SOUTH AUSTRALIA**

A.J. Fowler, R. McGarvey (editors)

South Australian Research and Development Institute
PO Box 120
Henley Beach 5022
South Australia



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Project No. 95/008

ISBN 0 7308 5258 X

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NON-TECHNICAL SUMMARY

95/008 Development of an integrated fisheries management model for King George whiting (*Sillaginodes punctata*) in South Australia.

Principal Investigator

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Objectives

1. To carry out a biological research program aimed at:
 - a. determining site-specific age structures by direct ageing of fish, and using this information for the estimation of demographic parameters;
 - b. completing the understanding of the life-history including reproductive, early and adult biological information;
 - c. assessing the genetic variation amongst populations over two spatial scales (i.e. amongst populations in the three southern mainland states and amongst regions within SA).
2. To review current commercial catch and effort information to:
 - a. identify the value of such data for estimating population abundance;
 - b. continue an on-going assessment of the impacts of technological advances in fishing equipment on catch and effort in the commercial sector of the fishery;
 - c. compare commercial catch with that from recreational catch information collected in SA using creel surveys in FRDC project 92/81.
3. To produce an age-structured, spatial-temporal fishery model for King George whiting in South Australia based on a comprehensive understanding of its biology, life-history and genetics as well as fishing statistics from the catch and effort database. The model will be used as a stock assessment tool to assess management options.

Non-technical summary

King George whiting (*Sillaginodes punctata*) remains a prime target species of the marine scalefish fishery of South Australia. Levels of fishing mortality are high on inshore populations throughout the fishery which has caused concern about the level of egg production. This prompted the need for a comprehensive stock assessment for this fishery. However, complicating this task is the fact that the life-history incorporates an obligate migratory step where fish move from shallow, inshore areas where they are heavily targeted, to deeper, more exposed places where the spawning populations occur.

The principal output of this project is a dynamic spatial model of the fishery, to be used for estimating performance indicators for annual stock assessment and for producing dynamic simulations for testing different management strategies. The annual stock assessments and the software for testing management simulations will be provided to the South Australian Marine Scalefish Management Committee, and fishery managers. The achievement of the spatial model depended on improving our understanding of the life-history of the species, and obtaining accurate estimates of demographic parameters. This was the primary aim of the biological research program.

For collection of biological data the South Australian fishery area was divided into three regions: Gulf St. Vincent; Spencer Gulf; and the west coast of Eyre Peninsula. Within each, adult fish from the

commercial or recreational fisheries were sampled on a regular basis, and used to generate age structures and for the analysis of reproductive biology. Fish were aged from their otoliths, using a validated ageing protocol. Population age structures were constructed for each locality and sampling occasion and used in the computer fishery model. In Gulf St. Vincent and Spencer Gulf, age structures became more complex from north to south, associated with a shift towards larger fish. In the simplest age structures the 3 year age class dominated, whilst the age range of the most complex was 3 - 17 years, with the 3 - 5 year classes the most abundant.

Reproductive biology was determined using a range of different techniques. All results suggested that King George whiting is a multiple batch spawner with asynchronous development, and indeterminate fecundity. Spawning occurred through the period of March to May, but was restricted to specific localities that were in relatively exposed locations, in deep water supporting reef habitat where the populations with the broadest age and size distributions were found.

Surveys of King George whiting post-larvae in chosen nursery areas were done monthly from July to October in 1995-1997, and early life-history characteristics were determined from analysis of the microstructure of otoliths. These data were used to suggest the locations of origin for larvae that recruited to different nursery areas. It appears that recruitment is likely the consequence of relatively local processes which in turn suggests that the South Australian populations of King George whiting consist of numerous, discrete, self-recruiting sub-populations.

Adult movement patterns were described through analysis of tag/recapture databases. Between the 1960s and 1980s approximately 26,000 fish were tagged throughout South Australia from which 1,589 recaptures provided useful information on movement. Fish tagged in Gulf St. Vincent and northern Spencer Gulf moved southwards over distances of up to several hundred kilometres. Alternatively, those tagged around Kangaroo Island, southern Spencer Gulf and in the west coast bays moved shorter distances and showed no systematic directional movement. There was little movement between the three fishery regions, with only 5 fish moving sufficiently far in an east/west direction to ultimately move from one region to another.

Population structure of King George whiting was analysed for samples of fish from Victoria, South Australia and Western Australia using mitochondrial DNA (mtDNA) sequences and nuclear DNA microsatellite allele frequencies. None of the studies demonstrated any phylogeographic structure. In effect there was no evidence of long-standing population structure and little evidence for contemporary population differentiation, although some results suggested that this was a recently expanded population.

Spatial and temporal trends in the commercial catch and effort data are described. Catch history is available from 1977 and targeted effort for the period of 1984-1998. There has been substantial reduction in fishing effort, for the three main gear types over the past 20 years but particularly for line fishing, which has resulted in some reduction in catch and value of the commercial fishery. There has also been a concomitant increase in CPUE in each fishery region. There is no comprehensive dataset for catch and effort in the recreational fishery. Data from one comprehensive survey done in 1995-96 suggest that recreational catch of King George whiting is approximately one third of the total, but the relative proportions taken by commercials and recreationals vary amongst regions, depending on proximity to major population centres.

Growth was estimated from age estimates from otoliths, which provided distributions of lengths at age over legally harvestable sizes for both sexes and the three regions. Mean length at age was modelled by a von Bertalanffy curve generalised by an exponent with sinusoidal seasonal variation. To alleviate any bias introduced by the cut-off in harvested samples at legal minimum length (LML), the normal likelihood distribution of length-at-age was truncated at the lower end by LML. Standard deviation was modelled by assuming a linear variation with age. Both mean length-at-age and individual length-at-age distributions yielded close fits. Growth slowed to near zero in winter, with females and Gulf St. Vincent showing fastest growth and largest maximum length.

Relatively high accuracy in describing region- and sex-specific distribution of lengths in each monthly age allowed the development of a new method of discrete subdivision of the population by length, in addition to age. Each cohort was partitioned into 'slices', the length range of the model cohort length-at-age distribution recruiting to the legal stock in each monthly age of growth. Because fishing mortality is very high, the numbers of different lengths surviving, which depends on the number of months those lengths of fish have been of legally harvestable size, can be explicitly accounted for. In fitting to the two principal data inputs, monthly catch totals by weight and catch-at-age samples from otoliths, the model predicted values are more accurately modelled with the length- and age-based description, yielding more precise and accurate estimates of mortality, and thus monthly and yearly population size.

Once-yearly January movements among 12 spatial cells were modelled by transition matrices. Movement transition probabilities were estimated from the 1,589 successful tag recaptures that were made during the 1960s-1980s. Movement was southward, directed towards the spawning aggregations in the two gulfs, with negligible movement among the three regions.

The principal goal of this project for decision making relating to resource management is to provide yearly performance indicators for King George whiting, to fishery managers. An overall fishery model estimator was developed, which outputs the following performance indicators: (1) yearly recruitment, (2) monthly exploitation rate, (3) monthly fishable biomass, (4) monthly total fishable population numbers, (5) yearly egg production. The performance indicator estimation model employs the growth and movement submodels and data sets described above. Fits to catches-at-age and monthly catch totals were good. Because southward migration from the upper gulfs was explicit, bias due to absence of older ages in observed catch-at-age distributions was obviated or reduced. Indicators above were obtained for each spatial cell.

Using the parameters and model equations of the estimator, a management strategy simulation was programmed and linked to a Delphi graphical user interface. This allows testing strategies such as; quota, and effort reductions or closures by month or model cell. The software, using mouse driven menus: displays the four principal time series outputs; provides the user control over all input parameters; allows the user the ability to graph a wide range of additional model outputs and data inputs; displays, when requested, the fits to all catch-at-age samples; and includes a small statistical package for analysis of input and output data. Casting the model simulation in a commercial-style Windows software allows its distribution and use directly by management decision makers.

CHAPTER 1. GENERAL INTRODUCTION

A.J. Fowler

1.1 Background

The King George whiting (*Sillaginodes punctata*) is a significant natural resource of southern Australia. There are fisheries in each of the southern mainland states of which the most significant is located in South Australia (Kailola et al. 1993). Here, although it has dropped to the second most valuable marine finfish species of the commercial sector, King George whiting remains the most heavily targeted species of the commercial and recreational sectors combined (Knight and Tsolos 1999). In the year for which recreational and commercial catches were compared (1994/95) the total catch was 783.6 tonnes of which the commercial sector contributed 65.6%, which was worth \$5.6 million (McGlennon and Kinloch 1997).

In the early 1990s there were indications of decreasing catch rates in the South Australian fishery, which raised considerable concern about the overall level of fishing pressure on fish stocks. Consequently, a workshop was convened in December 1993 to identify the then level of understanding of the biology and fishery of King George whiting. The workshop involved the Marine Scalefish group of SARDI as well as Dr. Norm Hall (WA Fisheries), who provided expert analysis and criticism of information and discussions. During this workshop, the only fishery model so far established for the King George whiting fishery, a yield-per-recruit (PRANA) model was reviewed (Anon 1994). The model predicted that the fishery is over-exploited in terms of yield and egg production, suggesting that egg production had been reduced to approximately 4 - 5% of the maximum spawning potential. The model also predicted that to raise egg production to a level of 20% of the maximum potential would require a 56% reduction in total fishing effort, if the current minimum legal length was retained.

The predictions of the PRANA model caused concern about the sustainability of the fishery. Nevertheless however, this model had to be considered cautiously because of its inherent limitations. This was not a time-variable model, did not provide a spatial breakdown of the fishery, did not incorporate recruitment, year class strength, population size or CPUE data (Anon 1994, Baker et al. 1994). In view of these limitations it was proposed at the workshop that a substantially better stock assessment methodology for King George whiting would be the development of an age-structured model that incorporated spatial and temporal variability in estimates of biological parameters as well as fishery statistics. Dr Hall made a preliminary attempt to construct such a model, but failed because of the lack of demographic information across the range of the fishery, and because the understanding of the life-history of the species was incomplete.

The project proposal submitted to FRDC aimed to develop such a complex model for King George whiting for South Australia. The timing of the project was fortuitous for redressing the shortcomings identified in the workshop. Firstly, at that time new personnel had arrived in South Australia with expertise in areas of: otolith preparation and interpretation for ageing adult and juvenile fish; the development of mathematical models to describe population and fishery dynamics; analysis of population genetics based on the most advanced biotechnological procedures for DNA analysis. Also, at that time two other FRDC projects were under-way in South Australia, which would provide fundamental information on catch rates and fishing mortality (92/81, 93/83). The concomitance of these circumstances provided an extraordinary opportunity for a collaborative, multi-disciplinary, multi-institutional project to comprehensively describe the biology and assess the fishery of King George whiting, and to construct an unusually refined model to describe the fishery.

1.2 Need

In the several years leading up to the submission of the proposal for this project to FRDC in late 1994 there was considerable concern about the status of the stocks of King George whiting (*Sillaginodes punctata*) in South Australia, with indications that egg production was dangerously low. It was thought that the persistent high exploitation of this species would place the stocks at risk of collapse. Consequently, SARDI scientists considered there was an urgent need for a critical stock assessment that involved both a comprehensive analysis of the biology of the species across the range of the fishery, and an assessment of the consequence for fish stocks of sustaining the current levels of commercial and recreational fishing effort.

1.3 Objectives

1. To carry out a biological research program aimed at:
 - a. determining site-specific age structures by direct ageing of fish, and using this information for the estimation of demographic parameters;
 - b. completing the understanding of the life-history including reproductive, early and adult biological information;
 - c. assessing the genetic variation amongst populations over two spatial scales (i.e. amongst populations in the three southern mainland states and amongst regions within SA).

2. To review current commercial catch and effort information to:
 - a. identify the value of such data for estimating population abundance;
 - b. continue an on-going assessment of the impacts of technological advances in fishing equipment on catch and effort in the commercial sector of the fishery;

- c. compare commercial catch with that from recreational catch information collected in SA using creel surveys in FRDC project 92/81.
3. To produce an age-structured, spatial-temporal fishery model for King George whiting in South Australia based on a comprehensive understanding of its biology, life-history and genetics as well as fishing statistics from the catch and effort database. The model will be used as a stock assessment tool to assess management options.

1.4 Rationale and Approach

The project proposal was submitted in December 1994. After a workshop involving managers, fishing representatives and South Australian and inter-state scientists that was aimed at identifying research priorities for the King George whiting (May 1995), the project was ultimately funded in late 1995. FRDC committed \$461,163 matching the combined contribution of SARDI (\$419,342) and the South Australian Museum (\$41,129). Some preliminary biological data had been collected in both 1994 and 1995, which augmented the main data collection period funded by this project of 1996 and 1997. The construction of the computer model commenced in early 1998 and proceeded through 1999. The results from the research project are summarised in the following chapters.

Chapters 3 - 7 summarise the results from the biological research program, and include: information on population structure; reproductive biology; both early and adult life-history information; estimates of post-larval recruitment; and an analysis of stock structure based on genetic variation. The following chapter on fishery trends presents the historical trends in catch, effort and CPUE at a broad geographic scale. Chapters 9 - 13 describe the various components of the population model, the analytical procedures applied to estimate these, and the processes involved in their estimation.

1.5 References

- Anon. 1994. A review of the King George whiting (*Sillaginodes punctata*) fishery in South Australia: status and research directions. SARDI Unpublished report. Workshop proceedings held on Dec 7th and 8th 1993. 20 pp.
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- Knight MA and Tsolos A (1999). South Australian Fisheries and Aquaculture Information and Statistics Report. SARDI Research Report Series.
- McGlennon D and Kinloch MA (1997). Resource allocation in the South Australian marine scalefish fishery. FRDC project 93/249, Final Report.

CHAPTER 2. GENERAL METHODS

A.J. Fowler

2.1 Sources of data

The data presented in this report were derived from numerous sources. The biological samples used to generate age and size structures and for the analysis of reproductive biology were obtained by: sub-sampling the commercial catch; from samples provided by recreational fishers; or from fish captured on scientific cruises. Inter-annual variation in the estimates of recruitment of post-larval fish were obtained from monthly surveys at particular times of the year. Patterns of adult movement were from the integration of results from the analysis of historical tag/recapture databases, from studies done between the 1960s and 1980s at numerous places around the state. Samples processed in the genetic analysis were collected as part of our field sampling program, whilst some were provided by other researchers in Victoria and Western Australia. Historical commercial catch and effort data were extracted from the GARFIS database.

2.2 Spatial Breakdown

The main fishery area for King George whiting in South Australia includes all inshore areas between Cape Jervis in the east to Denial Bay in the west, including Gulf St. Vincent, Spencer Gulf and Kangaroo Island. A variety of habitat types are offered throughout this extensive coastal area. Both Gulf St. Vincent and Spencer Gulf offer significant gradients in habitat type with the range in seasonal temperatures increasing northwards, whilst salinity also increases northwards, as is characteristic of inverse estuaries (de Silva Samarasinghe and Lennon 1987, Petrusevics 1993). Wave energy and depth decrease from the gulf entrances to the north. The relative cover of seagrass meadows, mainly *Posidonia* spp. and *Amphibolis antarctica*, compared with sand and rocky reef also increases northwards (Edyvane 1998).

The north-eastern coast of Kangaroo Island is characterised by shallow, protected bays supporting extensive seagrass meadows which give way westwards to steep, rocky coastline and deep, off-shore, low relief reefs (Shepherd and Sprigg 1976). The west coast of Eyre Peninsula is a high energy region which faces the prevailing south-west winds, but which incorporate several large, shallow bays which offer low energy, shallow habitats, that support extensive seagrass meadows (Edyvane 1998).

Because the ultimate aim of this study was to produce a spatial population model, the purpose of our biological sampling was to describe spatial variation in relevant characteristics across the whole

fishery. The area between Cape Jervis and Denial Bay was divided in different ways depending on the particular research topic.

1. For the analysis of fishery trends, data on commercial catch and effort were provided by individual fishers, for the particular South Australian Marine Fishing Area in which they had taken their catch (Fig. 2.1). These data were recorded and maintained as a general marine scalefish database (Garfis database). For analysis and presentation (Chpt 8), the data from some adjacent Marine Fishing Areas were combined to form seven fishery regions.

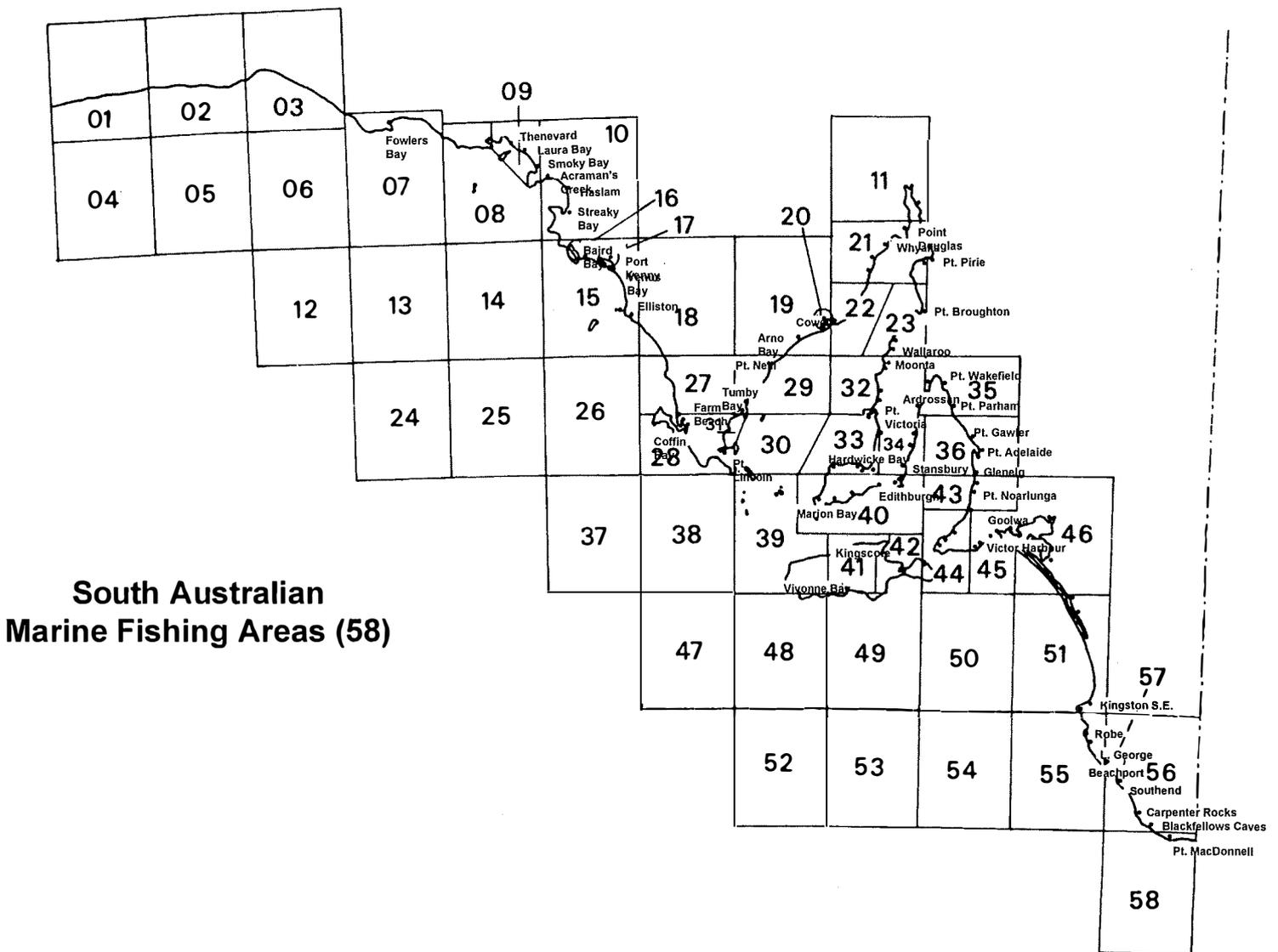


Fig. 2.1 Map of South Australia showing the 58 Marine Fishing Areas.

2. For the biological research program (Chpts 3, 4, 5, 6, 7) the fishery area was divided into three regions: an eastern region comprised of Gulf St. Vincent, Investigator Strait and the north coast of Kangaroo Island; the Spencer Gulf region; and a western region, i.e. the west coast of Eyre Peninsula (Fig. 2.2). Each region was sampled at a number of different localities, with each locality representing a substantial area that presented a characteristic habitat type.

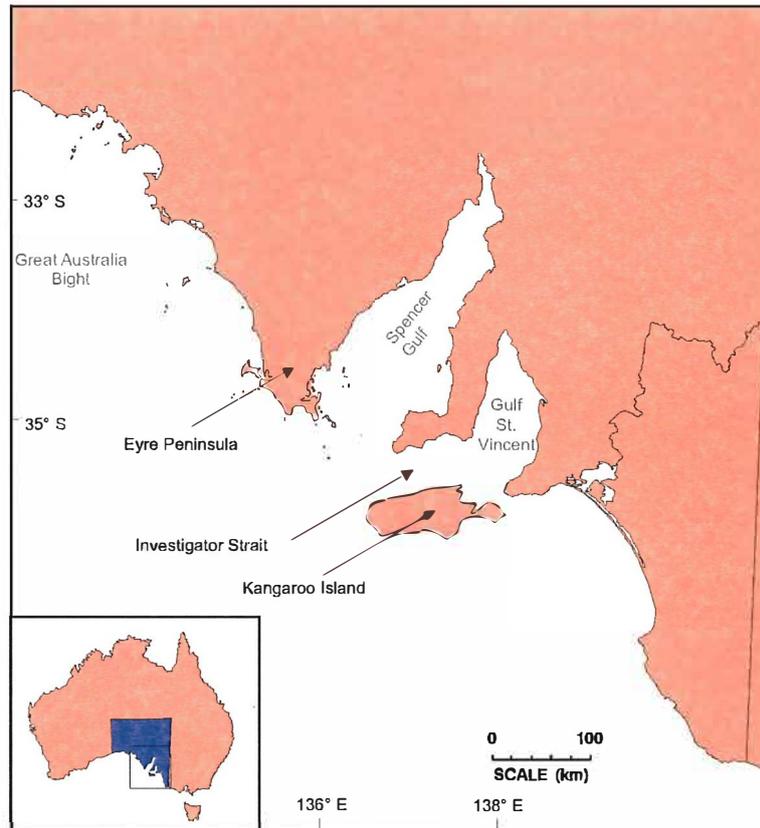


Fig. 2.2 Map of South Australia showing the three fishery regions: the eastern region; Spencer Gulf; and the west coast of Eyre Peninsula. Inset shows the main map area on the map of Australia.

3. In the population model the basic spatial unit is a “Movecell”. In total, there were 13 of these, where each represented a particular combination of Marine Fishing Areas (Fig. 2.3).

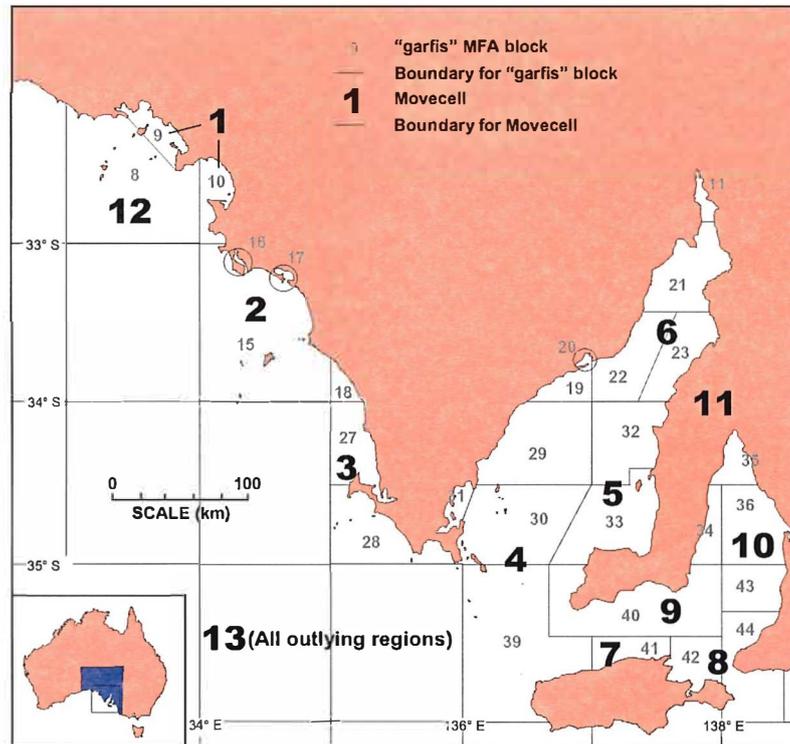


Fig. 2.3 Map of South Australia showing the Marine Fishing Areas and the 13 Movecells used in the population model. Inset shows the main map area on the map of Australia.

2.3 Temporal Breakdown

We attempted to collect biological information seasonally. However, since more effort was devoted to sampling during the reproductive season (Fowler et al. 1999, Fowler et al. 2000), higher numbers of samples, and individual sample sizes were taken at this time of the year.

2.4 References

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- Edyvane K (1998). Conserving marine biodiversity in South Australia. Part 2: Identification of areas of high conservation value in South Australia. Final report to Biodiversity Group (Environment Australia) for Project OR52 (Marine and Coastal Biodiversity strategy for South Australia).
- Fowler AJ, McLeay L and Short DA (1999). Reproductive mode and spawning information based on gonad analysis for the King George whiting (Percoidei : Sillaginidae) from South Australia. *Marine and Freshwater Research* 50: 1-14.
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CHAPTER 3. POPULATION STRUCTURE

A.J. Fowler

3.1 Introduction

The most comprehensive adult ageing study to date for King George whiting was done in Western Australia (Hyndes et al. 1998), which on the basis of otolith interpretation provided estimates of growth parameters and longevity for local populations. Despite several recent publications which incorporate some information on age determination and estimates of age (Fowler and Short 1998, Fowler et al. 1999), there remains a lack of published age-based information for the King George whiting in South Australia. Early ageing work in this state was based on the interpretation of scales (Jones et al. 1990), but over the past two decades the accuracy of this technique has been questioned for many species of finfish (Beamish 1992). Such concern about the technique diminishes the confidence that can be placed in growth and mortality relationships and estimates of longevity that are derived from the estimates of age, and this ultimately undermines the management protocols on which they are based (Beamish and McFarlane 1995). Also, there are as yet no published descriptions of the patterns of dispersion of King George whiting in South Australia, with respect to size and age.

In this study we have tried to redress the lack of age-based information for the King George whiting in South Australia. Estimates of age were based on the interpretation of the structure of otoliths, which still remain the preferred structure in studies on the direct ageing of fish. However, before otoliths can be used in a general ageing application the technique must be validated to ensure that age estimates are accurate and to assess the precision of otolith counts. In this study, such validation work was done and an ageing protocol developed for the King George whiting of South Australia.

Samples of fish were collected from which population age and size structures were developed for 12 localities representing the three geographic regions (Fig. 3.1), and a range of habitat types across South Australia. The specific objectives of this chapter were to:

To assess the usefulness of otoliths for ageing King George whiting of South Australia;

To present size and age structures and sex ratios for fished populations from 12 localities that represent the three main fishery regions.

3.2 Materials and Methods

Validation studies

To be useful for ageing purposes the otoliths of any fish species must fulfil three criteria (Fowler and Doherty 1992, Fowler and Short 1998). Several studies were done to assess these three criteria for the King George whiting, being aimed at determining: the periodicity of the formation of the opaque zone in otoliths; when the first increment is formed; and the characteristics of otolith growth. The three criteria, the methodological approach to their assessment and the results of this validation work are described in Fowler and Short (1998).

Population Size and Age Structures

The Gulf St. Vincent, Spencer Gulf and west coast fishery regions were each sampled at four localities which each displayed individual characteristics of habitat, topography and coastal physiography (Edyvane 1998). These are shown on Fig. 3.1, and the characteristics of their habitats summarised in Table 3.1.

Data presented here were collected only through the months of March to May in some years between 1995 and 1998, the three month period incorporating the main part of the spawning season in South Australia (Chpt. 4, Fowler et al. 1999). This is the time of year for which we have the largest sample sizes, and by restricting presentation to a specific time of year prevents confounding or smearing of spatial differences by temporal effects.

Processing fish samples

Most fish were obtained from the fishery and were therefore subject to a minimum legal size (28 cm TL prior to Sept 1995; 30 cm TL after Sept 1995). Such samples were collected in two ways: the commercial catch was sub-sampled at fish processing plants; or some whole fish were purchased from commercial processors (Table 3.1). Samples were usually in good condition and processed by us within 48 hours of capture. Other samples were collected on scientific cruises and processed within 4 hours of capture. Some frozen carcasses were also obtained from recreational fishers (Table 3.1).

Each fish was processed according to a standard protocol. It was measured for total and standard lengths (TL, SL) to the nearest mm, and when possible weighed to 0.1 g. The sagittae, the largest pair of otoliths, were removed through a transverse cut across the back of the fish's head, were cleaned, dried and stored in labelled plastic bags.

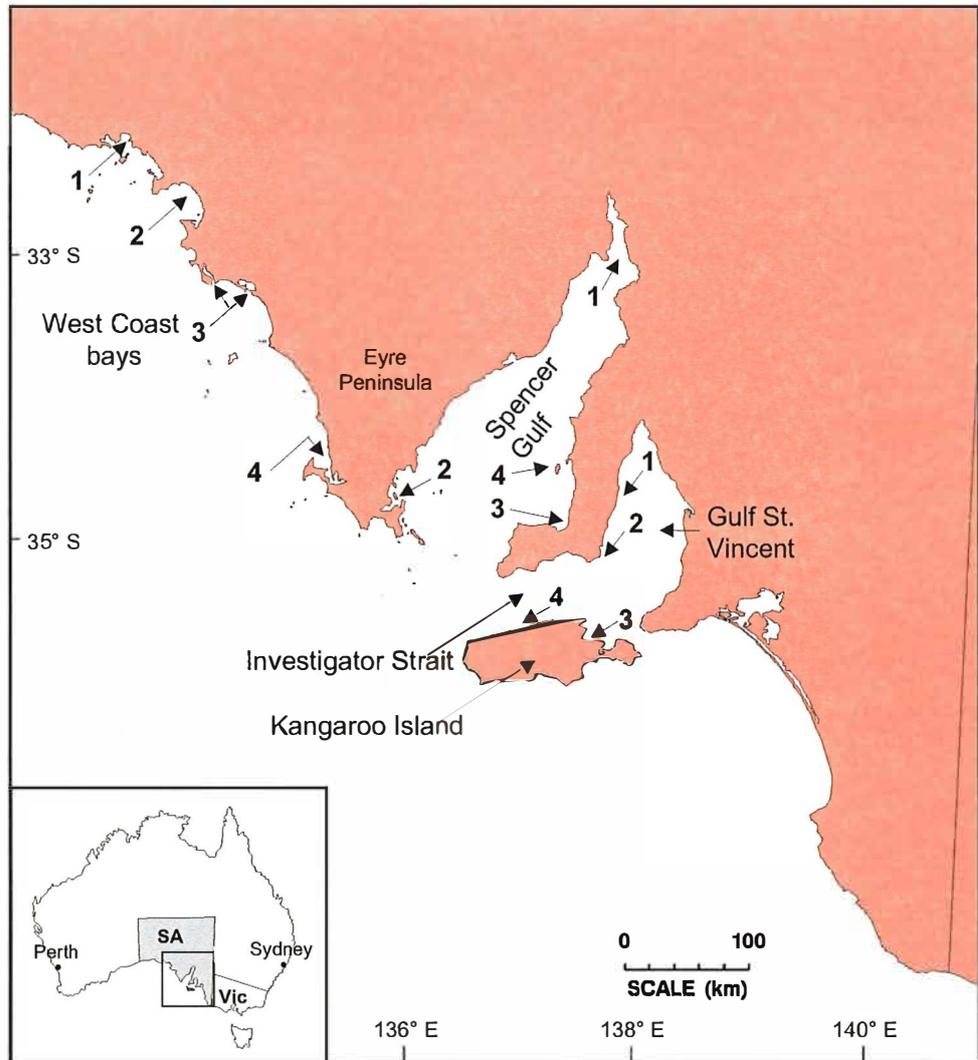


Fig. 3.1 Map of the main fishing area of South Australia showing the three regions sampled: the eastern region; Spencer Gulf; and the west coast bays. Information on the four numbered localities sampled per region is provided in Table 3.1. Inset shows the location of the main map as part of South Australia.

Table 3.1. Information on the localities sampled within the three regions, the habitats they present, the years they were sampled, the mode of collection and accumulated total of fish sampled through March, April and May of each year. For mode of collection C = sub-sampled from the commercial catch, P = purchased from the commercial fishery, R = obtained from recreational fishers, S = caught on a scientific cruise. Information on habitat and wave energy were obtained from Shepherd and Sprigg (1976), and Edyvane (1998).

Region	Locality number	Locality Name	Depth	Wave Energy	Habitat description	Year	Mode of collection	N	
Eastern	1	Port Vincent	<10 m	Low	Extensive seagrass meadows with patches of sand	1995	R	520	
						1996	R	515	
						1997	R	194	
	2	Tapley Shoal	9 m	Medium	Shallow shoal surrounded by seagrass meadows	1995	R	37	
						1996	R	117	
	3	Kangaroo Island - Inshore bays	<10 m	Low	Sheltered bays supporting seagrass meadows	1995	C	200	
						1996	C	169	
	4	Kangaroo Island North-coast	To 60 m Off-shore	Moderate/ High	Rocky coast dropping to deep water off-shore, sand with aeolianite reef and kunkarised shell beds	1996	C	238	
						1997	C	455	
						1998	C	127	
	Spencer Gulf	1	Northern Spencer Gulf	<10 m	Low	Large areas of sand & seagrass meadows	1996	R	139
							1997	C	198
2		Port Lincoln	<20 m	Low	Large, sheltered embayments, rocky headlands, off-shore islands with habitats of sand, seagrass and reef	1995	C	284	
						1996	C	332	
						1997	C	105	
3		Port Rickaby	<20 m	Low/ moderate	Large embayment, rocky headlands with sand, seagrass and rocky reef	1996	R	84	
						1997	R	320	
4		Wardang Island	<20 m	Moderate/ High	Sand, reef and Seagrass	1997	C/S	302	
	1998					C	199		
West coast Of Eyre Peninsula	1	Denial Bay	<5 m	Low	Sheltered embayment, mangroves, large area of seagrass, some sand and reef	1995	C	512	
						1996	C	319	
						1997	C	223	
	2	Streaky Bay	<10 m	Low	Sheltered embayment, mangroves, large area of seagrass, some sand and reef	1995	C	328	
						1996	C	164	
						1997	C	98	
	3	Baird & Venus Bays	<6 m	Low	Sheltered embayment, large area of seagrass, some sand and reef	1995	C	59	
						1996	C	254	
						1997	C	100	
	4	Coffin Bay	<7 m	Low	Large sheltered embayment, large area of seagrass, some sand and reef	1995	C	200	
						1996	C	50	
						1997	C	119	

Determination of fish age

Fish age was determined by analysis of otolith macrostructure based on a particular ageing protocol (Fowler and Short 1998). Small otoliths mainly from fish in the 2 – 3 year age classes were examined whole, immersed in water against a black background using incident white light. Annuli were counted along the dorsal/ventral axis towards the ventral edge. Ambiguous otoliths from young fish and otoliths from older fish were processed with a break and burn technique. The otolith was broken across the dorsal/ventral axis, and one half was slowly heated in a bunsen flame until the transverse surface had cooked through to be honey brown in colour. Immersion oil was smeared across this surface, which was then examined under white incident light at x6-x20 magnification. Opaque zones, which appear white against the orange/brown background in such preparations, were counted towards the proximal surface on the dorsal side of the sulcus (Fig. 4 in Fowler and Short 1998).

Population age and size structures were prepared by accumulating numbers per age or size class across months and years. Size structures were compared between both sexes using the Kolmogorov-Smirnov test.

3.3 Results

Validation Studies

The results from the validation studies involving marginal increment analysis and treatment of fish with tetracycline demonstrated that the first three opaque zones in the otoliths were formed annually (Fowler and Short 1998). However, since the increments in older otoliths displayed the same characteristics and involved the deposition of the same mass of otolith material as the earlier ones, suggests that these also were formed on an annual basis. The results also indicated that the first increment was deposited during spring/summer of the second year of life. Assuming a fixed birth date of 1st May (the mid-point of the spawning season), the first increment formed approximately 19 months after this date. A new increment was then formed each subsequent spring.

The characteristics of otolith growth and formation and the interaction with life-history meant that the structure of the otoliths of King George whiting in South Australia was directly related to fish age, and could therefore be used in a general ageing study. These characteristics of otolith growth and development were incorporated into an algorithm to calculate age in months from otolith counts, assuming a fixed birth-date of 1st May, and based on the number of increments counted and the time of year of fish capture. The algorithm was:

$Age_m = (N \times 12) + m_b + m_c$, where age_m = age in months, N = number of opaque zones, m_b = number of months from universal birth date (i.e. 1st May) to the end of year, m_c = number of months from the start of year to month of capture of the fish. The results of this validation study are described in full in Fowler and Short (1998).

Population Size and Age Structures

Through the period of 1995 to 1998 we measured and aged 13,000 fish. Of these, 6,961 were sampled from our nominated 12 localities through the months of March to May between 1995 and 1998. Such data demonstrated that population structure varied at several spatial scales, and that the spatial differences were consistent over a number of years.

Eastern Region

The fished population of King George whiting from the shallow, near-shore seagrass beds of the Port Vincent locality consisted of only three age classes, with the 3 year age class the most abundant (91.5% of all fish) (Fig. 3.2). Most of these fish were in the size range of 30 – 38 cm TL, and although the modal size for both sexes was 32 cm, there were significantly more females in the larger

size classes ($p = 0.0026$). At the inshore bays of Kangaroo Island the 3 year age class was also dominant (90.3% of all fish), although the fish were marginally smaller than those from Port Vincent (Fig. 3.2). Also here the size distributions did not differ between the sexes ($p = 0.1221$). Although the sex ratio was even at the inshore bays of Kangaroo Island a higher proportion of females were taken at Port Vincent (Table 3.2).

Population structure at both Tapley Shoal and in Investigator Strait north of Kangaroo Island was more complex. At the former locality, fish ranged from 3 – 6 years, and both sexes had modal sizes of 40 cm TL (Fig. 3.2). At the latter locality the age range was 3 - 17 years, with the 3 – 5 year classes most abundant. More older males were caught than females, with a negligible number of females older than 11 years. Sizes ranged from 32 – >50 cm TL and although modal sizes of both sexes were similar at 38 cm, males were relatively more abundant in smaller size classes and females in the larger (at Tapley Shoal $p = 0.0161$, at Kangaroo Island $p = 0.0017$). At Tapley Shoal the sex ratio of the catch was biased towards females, but at Kangaroo Island it was even when calculated across all three years, although one sex clearly outnumbered the other in each year (Table 3.2).

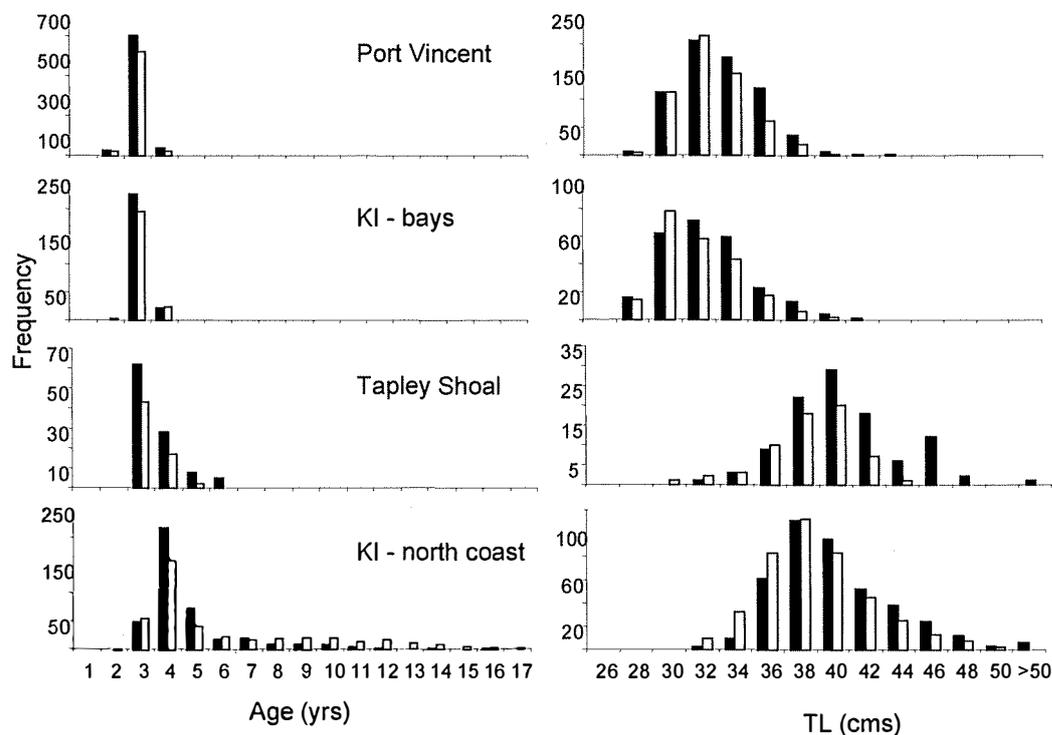


Fig. 3.2 Age structures and size frequency distributions for King George whiting sampled from four localities in the eastern region accumulated across years (shaded bars, females; light bars, males).

Spencer Gulf

At the northern locality three age classes were represented, with the 3 year age class clearly dominant for both sexes (96.1% of total) (Fig. 3.3). Although the size range was 28 – 40 cm, the modal size was 30 cm. Both sexes were evenly distributed amongst the size classes ($p = 1.000$), although there was a substantially higher number of females caught than males (Table 3.2).

At the three southern localities population structure was more complex. At Port Lincoln ages ranged from 3 to 6 years. Males had a modal size of 34 cm and were more numerous in the smaller size classes ($p = 0.0034$), while females with a modal size of 36 cm, dominated the larger size classes. At Port Rickaby fish were slightly larger than at Port Lincoln possibly because the 4 year age class was relatively more abundant (Fig. 3.3). Again, the larger fish were dominated by females ($p = 0.0354$).

Off-shore in south-eastern Spencer Gulf (Wardang Island, Corny Point), most fish were from 36 – 42 cm TL with the mode around 38 – 40 cm TL (Fig. 3.3). The larger sizes were dominated by females ($p = 0.0001$). Numerous age classes from 3 – 14 years were represented, but there were more older males than females. The 4 year age class was the most abundant and accounted for 58.4% of the total of 500 fish.

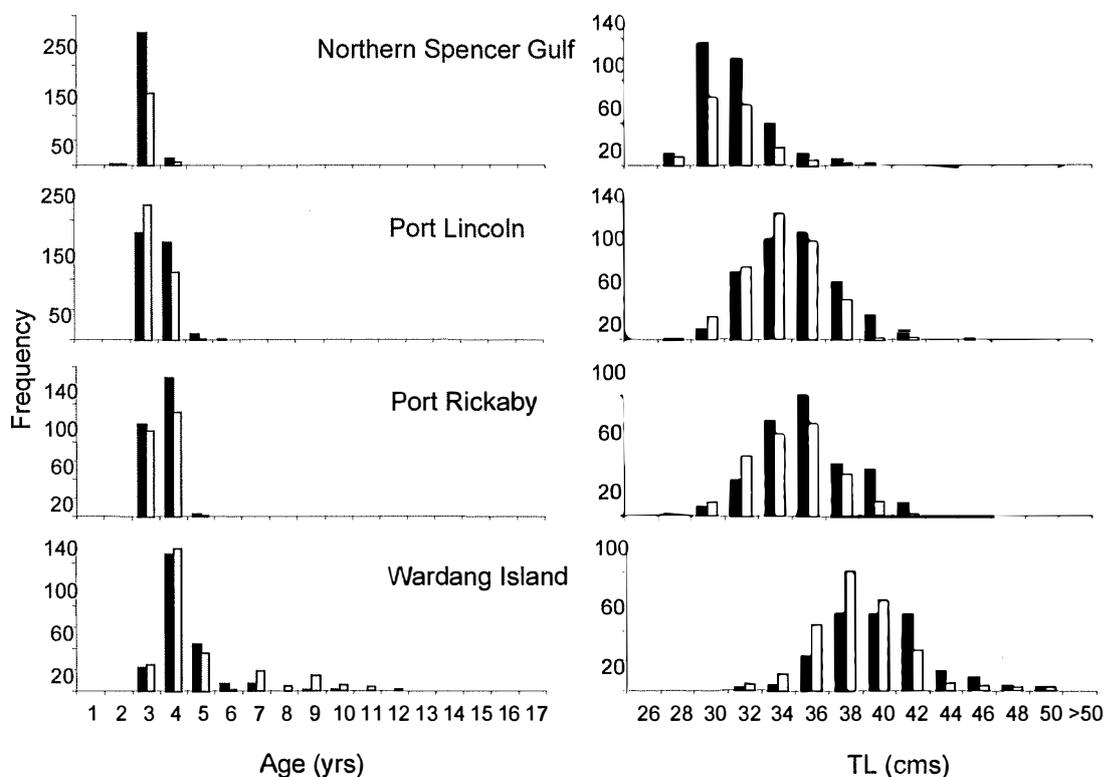


Fig. 3.3 Age structures and size frequency distributions for King George whiting sampled from four localities in Spencer Gulf accumulated across years (shaded bars, females; light bars, males).

Table 3.2 Results of the analysis of sex ratios for fish sampled during the reproductive seasons at each locality between 1995 and 1998. The Chi-square tests compared the totals of both sexes accumulated across years (* indicates significant at P = 0.05).

Region	Locality	Year	Total	Females	Males	X ²	P
GSV	Port Vincent	1995	520	279	241	9.6672 ₍₁₎	0.0019*
		1996	515	285	230		
		1997	194	105	89		
			1,229	669	560		
	KI – inshore bays	1995	200	110	90	1.9756 ₍₁₎	0.1599
		1996	169	88	81		
			369	198	171		
	Tapley Shoal	1995	37	22	15	10.3896 ₍₁₎	0.0013*
		1996	117	75	42		
			154	97	57		
	KI - north coast	1996	238	74	164	0.0439 ₍₁₎	0.8340
		1997	455	248	207		
1998		127	91	36			
		820	413	407			
Spencer Gulf	Nth Spencer Gulf	1996	139	104	35	32.7151 ₍₁₎	0.0000*
		1997	198	117	81		
			337	221	116		
	Port Lincoln	1995	284	148	136	0.4008 ₍₁₎	0.5267
		1996	332	178	154		
		1997	105	43	62		
			721	369	352		
	Port Rickaby	1996	84	50	34	4.7921 ₍₁₎	0.0286*
		1997	320	174	146		
			404	224	180		
	Port Victoria	1997	302	140	162	0.4491 ₍₁₎	0.5028
		1998	199	103	96		
		501	243	258			
West coast	Denial Bay	1995	512	261	251	0.4592 ₍₁₎	0.498
		1996	39	166	153		
		1997	223	111	112		
			1,054	538	516		
	Streaky Bay	1995	328	159	169	0.8203 ₍₁₎	0.3651
		1996	164	86	78		
		1997	98	39	59		
			590	284	306		
	Baird & Venus	1995	59	34	25	2.3269 ₍₁₎	0.1272
		1996	254	133	121		
		1997	100	55	45		
			413	222	191		
Coffin Bay	1995	200	102	98	2.6043 ₍₁₎	0.1066	
	1996	50	28	22			
	1997	119	70	49			
		369	200	169			

West Coast

The bays on the west coast are shallow, protected and support extensive beds of seagrass. The local populations of King George whiting consisted of only a few age classes, each dominated by the 3 year age class (Fig. 3.4). Size structures, however, showed some spatial variation. Samples from Denial and Streaky Bays ranged primarily from 30 to 38 cm, with modes for both sexes at 34 cm. At the former locality the size distribution was even between the sexes ($p = 0.0724$), but at Streaky Bay they differed significantly ($p = 0.0140$). At Baird and Venus Bays ($p = 0.6783$), as well as Coffin Bay ($p = 1.000$), the sexes were distributed evenly between size classes, with both dominated by small fish which rarely exceeded 34 cm. Sex ratios were also relatively even at each locality (Table 3.2).

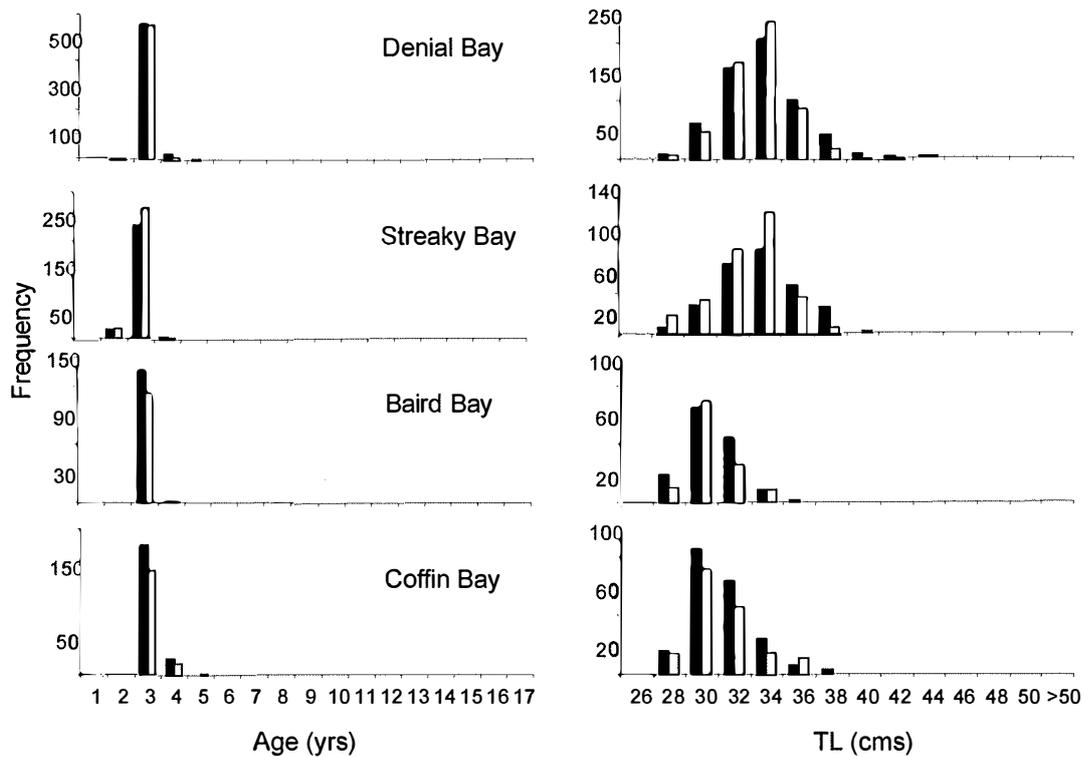


Fig. 3.4 Age structures and size frequency distributions for King George whiting sampled from four localities on the west coast accumulated across years (shaded bars, females; light bars, males).

Temporal Variation in Size and Age Structures

The size and age structures of catch from the fishery, as presented above, indicated that the populations from both gulfs and the west coast bays were based almost exclusively on fish from the 3 year age class that were relatively small. In contrast, along the north coast of Kangaroo Island and in Hardwicke Bay of Spencer Gulf the populations also contained some larger fish from a broader age range. These represented multi year-class fisheries with fish up to 17 years of age, with the older age classes well represented in the population. Since the data presented in Figs 3.2 and 3.3 were composites from data collected across several years, we considered it useful to examine the information presented for each individual year.

North coast of Kangaroo Island

The samples collected from the north coast of Kangaroo Island varied greatly in sex ratio between years with catches in 1996 dominated by males (M:F; 0.69:0.31) but those in both 1997 (0.46:0.54) and 1998 (0.28:0.72) dominated by females (Fig. 3.5). The size frequency distributions of females ranged from 320 to >500 mm TL, with modal sizes of 380 (1997) and 400 mm TL (1996, 1998) (Fig. 3.5). Age structures for females were dominated by young fish, although numerous older individuals were present. The most abundant age class in 1996 was the 3+'s, in 1997 the 4+'s and 1998 the 5+'s, suggesting a strong year class was moving through the age distribution. The proportion of the age structure comprised of old fish varied from year to year (fish > 5yrs comprised 37.8% in 1996, only 9.3% in 1997 and 23.1% in 1998). Despite this, there were significant positive correlations between the three age structures when lagged either by one year (i.e. 1996 vs 1997, $r = 0.8362$, $p = 0.0013$; 1997 vs 1998, $r = 0.6840$, $p = 0.0203$), or two years (i.e. 1996 vs 1998, $r = 0.9167$, $p = 0.0000$). These positive correlations suggest that variation amongst year classes was retained and manifested in the age structure from year to year.

The catch of males taken in 1996 covered a broad age range and the older classes were well represented (36% < 6 yrs; 64% > 5 yrs). In 1997 and 1998 the age structures were dominated by young fish, particularly the 4+ age class in 1997. The age structures reflect the strong year class as the 3+ age class in 1996, and the 4+ and 5+ age classes in 1997 and 1998 respectively.

South-east Spencer Gulf

In the deep, off-shore areas of Hardwicke Bay, including Wardang Island and Corny Point fish were generally large, ranging from 320 to 500 mm TL (Fig. 3.6). The modal size of females was 400 to 420 mm, and that of males was 380 mm. The catch of females in 1997 was dominated by the 4 year

age class, with only 11.2% of the sample being older than 5 years. In 1998 the 4 year age class was again dominant, and there were fewer older fish than in the previous year.

In 1997 the 4+ age class was most numerous for males, and there was a long tail in the distribution to the older fish. Those older than 5 years comprised >32% of the catch. However, in 1998 no males older than 5 years were caught.

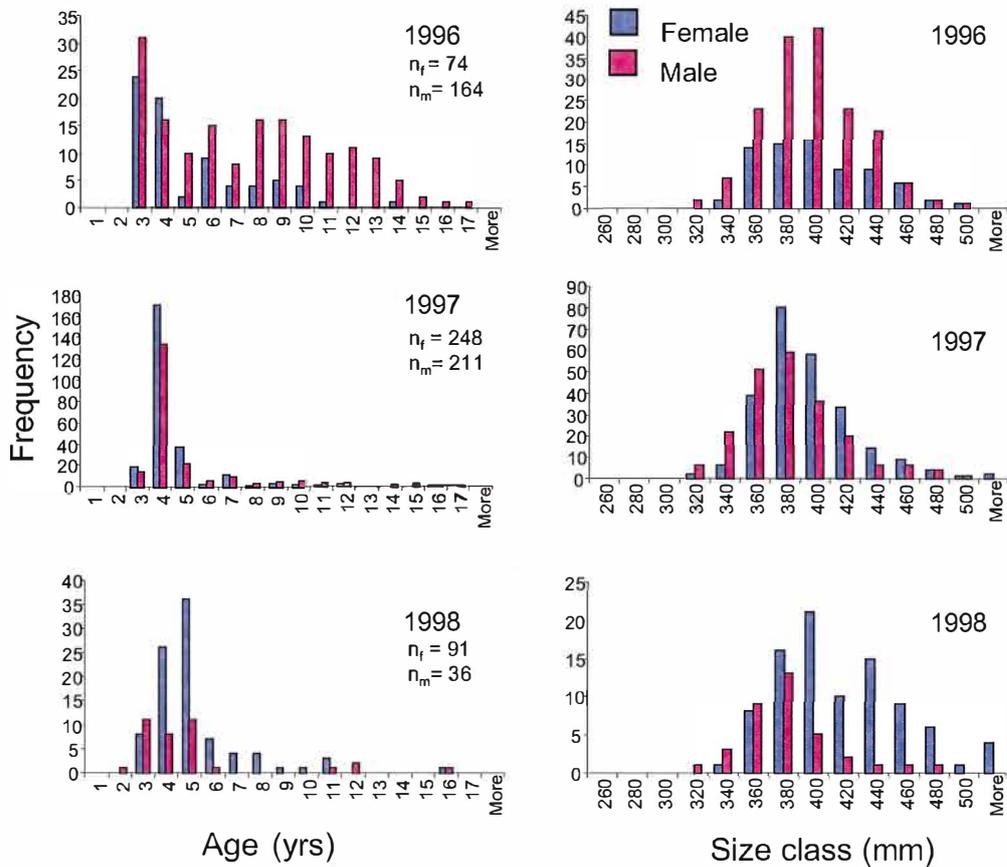


Fig. 3.5 Age and size structures of samples from the commercial fishery from the north coast of Kangaroo Island through March to May of 1996 to 1998 (n_f = number of females, n_m = males).

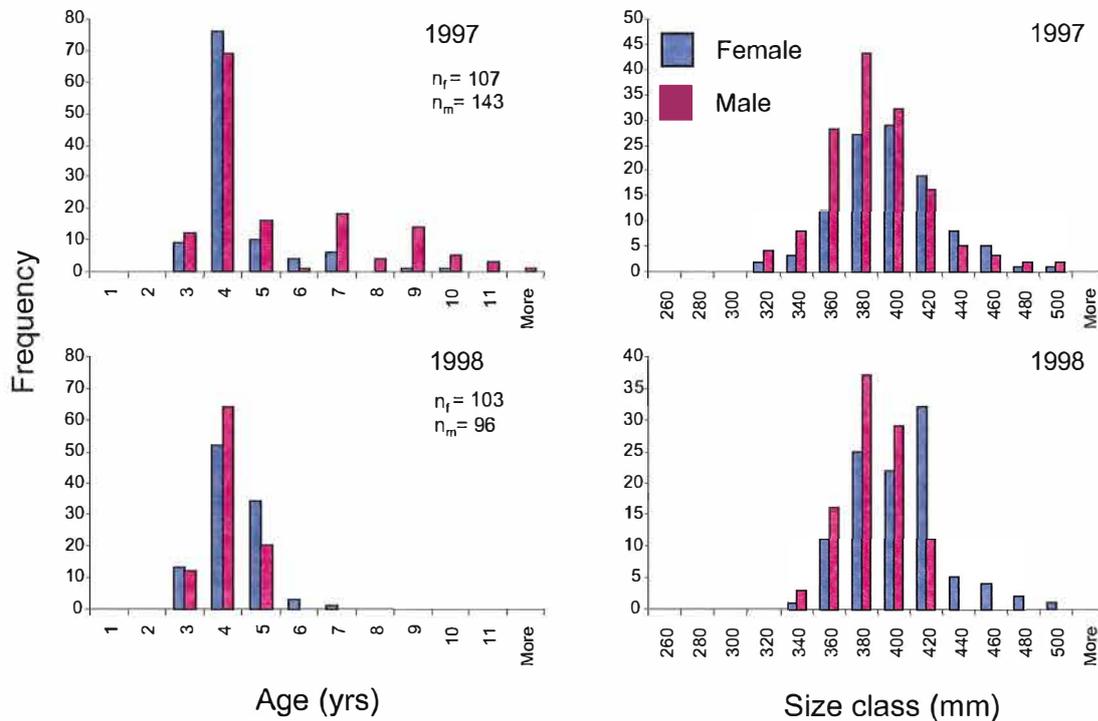


Fig. 3.6 Age and size structures of samples from the commercial fishery from south-eastern Spencer Gulf through March to May of 1997 and 1998 (n_f = number of females, n_m = males).

Variation through one year

For those fisheries dominated by a single year class of three year olds (i.e. Gulf St. Vincent, northern Spencer Gulf, and all west coast bays), it should be possible to determine when one year class is replaced by that of the following year. Our best opportunity to determine this was provided by a number of samples from Denial Bay collected throughout 1995 (Fig. 3.7). The resulting age structures from between February and June were clearly dominated by the 3 year age class (i.e. that spawned in 1992), with small numbers of both younger and older fish. However, the samples taken from August onwards demonstrated the replacement of this 3 year age class by the year class spawned in 1993. By December almost 100% replacement of the 1992 year class had occurred.

3.4 Discussion

Spatial variation in population characteristics

The size and age structures of King George whiting differ throughout the coastal waters of South Australia. The fished part of populations (i.e. >30 cm TL) in the two northern gulfs and the west coast bays consisted largely of the 3 year age class, which generally constituted >90% of the catch through the period of March to May. At the southern end of both gulfs population structure became marginally more complex, since the 4-6 year age classes also contributed to the fishery, resulting in broader size distributions. At several off-shore, southern localities population age structure was most complex, with ages from 3 to 17 years. This maximum age still underestimates the longevity, since the oldest fish so far aged in South Australia was 22 years old (Noell 1997). Compared with other species of sillaginids (e.g. Burchmore et al. 1988, Hyndes and Potter 1997), these data reinforce that King George whiting is the longest lived and largest species of this family in Australia (Hyndes et al. 1998).

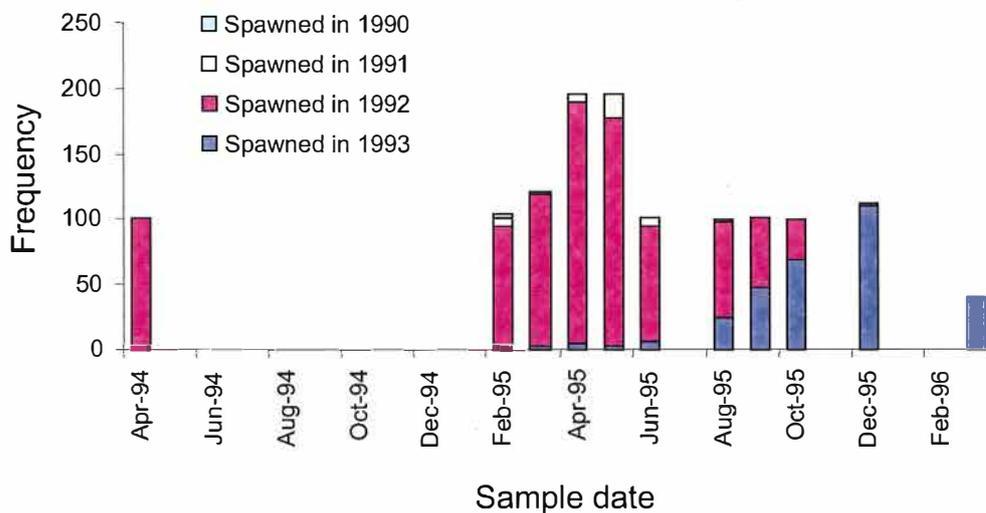


Fig. 3.7 Number of fish per year class caught on each sampling occasion in 1995 and 1996 from Denial Bay.

The changes in complexity of population age and size structures were associated with ontogenetic shifts in habitat use. The simplest age structures were found at places adjacent to nursery areas, that were typically shallow and supported extensive stands of the seagrasses *Posidonia* spp. and *Amphibolis antarctica*, where fish are associated with the patchy mosaic of seagrass and sand. Around Tapley Shoal, Port Lincoln and Port Rickaby, where water is deeper and there is more rocky reef, older and larger fish occur. The most complex populations of King George whiting, however, were associated with off-shore reefs, shoals or large mounds in relatively deep water in exposed locations that experience medium/high wave energy.

The related changes between population structure and habitat occurred at several spatial scales, depending on the distance between habitat types. At Kangaroo Island the habitats appropriate for post-larvae, juveniles, sub-adults, and mature older adults are contiguous along the northern coastline, over a distance of only 10's of kilometres. Alternatively, in both Gulf St. Vincent and Spencer Gulf, the habitat change is gradual from north to south (Edyvane 1998), which is associated with a change in population characteristics of King George whiting. Similarly, around Perth, Western Australia, ontogenetic shifts in habitat associations are typical of several sillaginid species and changes in population structure occur over relatively short distances between inshore and off-shore locations (Hyndes et al. 1996). *Sillaginodes punctata*, *Sillago bassensis*, *S. vittata* and *S. berrus* all display size-related shifts from the near-shore (< 1.5 m) to deep, inner shelf waters. Large King George whiting up to 14 years of age were found associated with off-shore limestone reefs at 6 – 50 m in deep (Hyndes et al. 1998).

Temporal variation in size and age structures

Our analysis of the temporal variation in population age structures demonstrated a number of characteristics. Ages ranged from 3 to 17 years; year class strength varied considerably; and there was some indication that year class strength was retained and manifested in age structures from year to year.

Our estimates of age structures also demonstrated substantial inter-annual variation, e.g. the sample from the north coast of Kangaroo Island in 1996 contained a high proportion of old fish, but that from 1997 was almost exclusively less than 6 years old. It is unlikely that such variability reflects a real shift in population age structure, but more likely reflects small scale patchiness in the distribution patterns of fish with respect to sex, size and age.

Variation through one year

At Denial Bay the fishery essentially consists of a single year class, typical of other shallower, inshore places in both South Australia and Victoria (Smith and McDonald 1997). Our analysis of population structure over several months through 1995 indicated that the change-over in year classes in the fishery took place gradually between June and December. By December essentially 100% of the fishery consisted of the new year class. There are several hypotheses to account for this phenomenon: The older year class may be essentially wiped out by the fishery, whilst the younger one gradually becomes more and more vulnerable to the fishery;

Alternatively, since ontogenetic movement patterns are an important part of the life-history of this species (Chpt. 6), the fish in the older year class may gradually move away from inshore areas, and are replaced by the younger year class coming out of the nursery areas.

3.5 References

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CHAPTER 4. REPRODUCTIVE BIOLOGY

A.J. Fowler

4.1 Introduction

Previous work on the reproductive biology of the King George whiting in South Australia provided preliminary estimates of size-at-maturity, fecundity and time-of-spawning (Scott 1954, Cockrum and Jones 1992). However, as yet our understanding of reproductive biology remains poor and there is insufficient information to make definitive statements about the mode of ovary development, its relationship with spawning frequency, as well as which fish spawn, and where and when this occurs.

This chapter is concerned with addressing these general questions based on data collected through the period of 1995 to 1998. The specific objectives were:

1. to describe the geographic variation in the reproductive characteristics of the King George whiting populations across South Australia;
2. to determine the likely reproductive mode of King George whiting by a detailed analysis of the gonad characteristics at those places where gonad development culminated in spawning. This study included:
 - a. confirming whether the period of March to May is an important spawning period;
 - b. analysis of the organisation of oocytes at different developmental stages. Such data were used to determine whether this species is a single or multiple batch spawner, and if annual fecundity is likely to be determinate or indeterminate;
 - c. interpretation of the microscopic characteristics of ovaries to divide mature females into spawners and non-spawners, calculate the fraction of females that spawn at particular times, and use this information to estimate the spawning frequency;
 - d. to estimate batch fecundity and determine its relationships with fish size and age.

4.2 Materials and Methods

Geographic variation in reproductive characteristics

Each fish that contributed to the analysis of size and age described in Chapter 3, was also sexed and examined for its state of reproductive development. This spatial and temporal breakdown of gonad characteristics is presented in this chapter.

For each fish the gonads were removed, sexed and weighed to 0.1 g. Gonosomatic indices (GSI) were calculated as: $GSI = [W_g / W_f] * 100\%$ (W_g = gonad weight, W_f = gonad-free fish weight). Ovaries were classified macroscopically to one of five stages of development, based on size, colour and visibility of oocytes (Table 4.1), which effectively distinguished between undeveloped and developing females. However, more detailed analysis from some developing ovaries was achieved by histological preparation and microscopic examination. For such ovaries (N = 472), a segment was removed from the centre of one lobe and preserved in a fixative of formalin, acetic acid and calcium chloride (FAACC). For males there was a lack of discrete maturity stages so they were classified only into those that showed no testicular development (testes remained as black threads), and those that displayed at least a minimal level of development (thickening of gonad or change in colour towards grey).

For some ovaries that were initially classified as Stages 3 or 4 (Table 4.1), the second ovary was used to determine size frequency distributions of oocytes and to estimate batch fecundity. This ovary was weighed, split longitudinally along the long axis and the oocytes were washed from the ovary matrix, collected in a 100 μ m filter, transferred to a storage jar and preserved in 500 ml of a 2% formalin solution (Lowerre-Barbieri and Barbieri 1993).

Laboratory analysis of preserved samples

Histological preparations

From the FAACC-preserved tissue, histological sections were prepared for microscopic analysis. Tissue was sectioned at 6 - 7 μ m, and stained using haematoxylin and eosin. Slides were examined at x100 magnification and classified according to: the most advanced stage of oocyte development; level of atresia; and presence/absence of post-ovulatory follicles (Farley and Davis 1998). The former were classified as; unyolked, partially yolked, advanced yolked,

migratory nucleus or hydrated (Table 4.2). The abundance of α -atretic oocytes relative to advanced yolked ones was estimated as; no atresia, <10%, 10-50%, >50% and 100%. The presence/absence of post-ovulatory follicles was noted, along with a qualitative assessment of their age, based on the presence/absence of a lumen and the level of disruption to the arrangement of thecal and granulosa cells (Table 4.2).

Table 4.1. Macroscopic stages of development of ovaries of King George whiting. The microscopic characteristics of these stages, as determined from histological preparations, are also provided based on stages of oocyte development from Table 4.2.

Stage	Macroscopic appearance	Microscopic characteristics
1- Immature	Ovaries small, undeveloped, clear, jelly-like or glassy, grey to pink in colour	Only unyolked and non-atretic oocytes
2 – Developing	Ovaries small, opaque, light yellow in colour – individual oocytes are not discernible	Mainly unyolked and a few partially yolked oocytes, with no major atresia
3 – Developed	Ovaries relatively large, and quite turgid, yellow to orange in colour - individual oocytes are discernible	Oocytes at several phases - unyolked, partially yolked, but dominated by advanced. Maybe some minor atresia of advanced yolked oocytes
4 - Gravid or running ripe	Ovaries large, orange. Clear hydrated oocytes are visible amongst opaque oocytes. Oocytes may be ovulated	Oocytes present at all stages from unyolked to hydrated. Some atretic oocytes and POFs may be present, but generally dominated by advanced yolk and hydrated oocytes
5 - Regressing or resting	Ovaries are small to medium – mustard yellow/orange/reddish in colour. More flaccid than previous stages, and have a granular appearance	Oocytes of all stages may be present however there is a high incidence of atresia suggesting the end of spawning. POFs were not found at this stage

These microscopic characteristics were used to divide mature females (Stages 2-5 in Table 4.1) into spawning categories. Ovaries with migratory nucleus or hydrated oocytes or that had post-ovulatory follicles were considered to display evidence of spawning activity. Those without these were classified as not spawning, whilst those for which atresia exceeded 50%, were classified as regressing. For several fish, the sizes of oocytes at different stages of development were recorded from histological preparations. Oocytes sectioned through the nucleus along several transects across transverse sections were measured, from which size frequency distributions were determined.

Mature females (Stages 2-5) were classified into spawning and non-spawning fish, and used to calculate spawning fraction in two ways. Firstly, those that would have or did spawn on their day of capture, were recognised by having migratory nucleus or hydrated oocytes, or

new post-ovulatory follicles. Secondly, those that had spawned prior to the day of capture were characterised by having old post-ovulatory follicles (Table 4.2). The spawning fraction was the proportion of mature females in either of these two categories. Estimates of spawning fraction were used to provide a mean seasonal estimate of spawning frequency.

Table 4.2. Descriptions of each stage of development of oocytes, α -atretic oocytes and post-ovulatory follicles, modified from descriptions of Hunter and Macewicz (1985).

Stage	Microscopic characteristics
1- Unyolked	Oogonia are small, cytoplasm is basophilic. The nucleus is large, centrally located, several nucleoli occur at the nucleus periphery. Sizes were less than 136 μm (371 oogonia measured from 4 ovaries).
2 - Partially yolked	Similar to Stage 1, but larger with lipid granules throughout the cytoplasm. The follicular layer consists of two cell layers, and the zona radiata is present but still thin. Size range 71 – 291 μm (N = 164, 4 ovaries).
3 – Advanced yolked	Oocytes are large, with both lipid granules and eosinophilic yolk protein granules throughout the cytoplasm. The nucleus is still centrally located. The zona radiata is thick and highly eosinophilic. Size range 175 – 433 μm (N = 148, 4 ovaries).
4 – Migratory nucleus	As with Stage 3, except the nucleus is no longer centrally located but has migrated to the peripheral cytoplasm. This represents the initiation of the hydration process.
5 – Hydrated	The oocytes are much larger with uptake of fluid, the nucleus is absent, and yolk plates occupy the entire volume of the cytoplasm, then fuse to form a homogeneous mass. The zona radiata and follicular layers become greatly stretched. Size range 720 – 1,055 μm (N = 769, 9 ovaries).
α -atretic oocyte	The zona radiata dissolves, oocyte shape loses integrity. Yolk globules begin to disintegrate and are less regular in shape.
Post-ovulatory follicle (new)	This consists of the remaining follicle soon after ovulation. It is large, highly convoluted with an obvious lumen, and may contain fine granular material. The layered nature of both cell types (thecal and granulosa) remains intact.
Post-ovulatory follicle (old)	The convoluted nature is much less apparent, the lumen is much reduced, even closed, and the thecal and granulosa cells no longer retain their orderly arrangement.

Whole preserved oocytes

Formalin-preserved samples were used to obtain counts of oocytes, using a volumetric method. The sample was washed through a 100 μm sieve to remove the preservative, after which the oocytes were placed in water, making the volume up to 1,000 ml. Ten sub-samples of 1 ml were then examined under a binocular microscope using transmitted light. For some ovaries, all oocytes $>250 \mu\text{m}$ were counted and measured, whilst estimates of batch fecundity ($\pm\text{SD}$) were based only on the number of hydrated oocytes (diameter $>720 \mu\text{m}$), and calculating up to the full sample volume and combined weight of both ovaries.

4.3 Results

Geographic Variation in Gonad Development

Eastern Region

Weights of ovaries from fish collected during the reproductive season from Port Vincent and the bays of Kangaroo Island were very low with few exceeding 2.0 g, whilst testes rarely exceeded 1 g (Fig. 4.1). Whilst 14.4 and 7.1% of females from the two localities respectively had either developing or developed ovaries, these were classified to macroscopic stages 2, 3 or 5 (Table 4.3). None were classified to Stage 4, that would be indicative of spawning fish. A combined total of 38 ovaries from both localities were examined microscopically, and none displayed either hydrated oocytes or post-ovulatory follicles, which would be indicative of spawning (Table 4.3). Consequently, neither the macroscopic or microscopic analyses demonstrated evidence of “spawning” fish. A total of 28.6% and 12.3% of males respectively had developing testes (Table 4.3), but none were running ripe.

In contrast, the analysis of gonads from Tapley Shoal and the north coast of Kangaroo Island provided substantial evidence of spawning activity. At the latter locality most ovaries weighed between 5 – 25 g, with some up to 100 g, and most pairs of testes ranged from 5 to 50 g (Fig. 4.1). Ovaries were classified to all macroscopic stages of development including some at Stage 4 (Table 4.3). Of 201 ovaries from both localities examined microscopically, 71 displayed hydrated oocytes and 136 had post-ovulatory follicles, and were thus classified as “spawners”. A total of 95.3% of the 407 males from Kangaroo Island and 56.1% from Tapley Shoal had developing testes with many running ripe at the time of capture (Table 4.3).

Spencer Gulf

At the northern locality most ovary weights were <2 g and teste weights < 1 g (Fig. 4.2). Only 2.7% of these ovaries showed a sign of development, but no ovary displayed hydrated oocytes or post-ovulatory follicles (Table 4.3). Consequently the few developing females were classified as non-spawning. At both the south-west and south-east inshore localities most ovary weights were <4 g, and few of the remainder exceeded 10 g (Fig. 4.2). There were 18.2% of females in the south-west and 23.2% in the south-east with developing or developed gonads, but none was classified as spawning (Table 4.3). Furthermore, of the 28 ovaries from Port Lincoln examined microscopically none displayed the hydrated oocytes or post-ovulatory follicles, that would be indicative of spawning (Table 4.3). High proportions of

males were developing, but no fish was ever running ripe and testes generally weighed less than 4 g (Fig. 4.2).

Table 4.3 Results of the macroscopic interpretation and microscopic analysis of fish gonads. For males Stage 1 represents immature, >1 indicates at least a minimal level of testicular development. For females the 5 macroscopic stages are described in Table 4.1. The results of the histological analyses show the number of ovaries with the most advanced development stage as advanced yolked oocytes (AYO), as migratory nucleus (MN) or hydrated (H) oocytes and the number that were regressing (Regress). Also shown is the number of fish that had post-ovulatory follicles (POF's).

Region	Locality	Year	Males		Female – Macroscopic stages					Histological analyses					
			1	>1	1	2	3	4	5	AYO	Mn or Hy	Regress	POF's		
Eastern	Port Vincent	1995	204	37	250	26	3				2				
		1996	150	80	233	15	20		17	10		9			
		1997	46	43	90	9	6			5					
	Kl-inshore bays	1995	85	5	105	5				5		1			
		1996	65	16	79	6	3			6					
	Tapley Shoal	1995	11	4	11	4	7			2		2			
		1996	14	28	39	8	18	1	9	7	1	9			
	Kl-north coast	1996	0	164	3	8	17	18	18	9	36	2		3	
		1997	17	190	63	33	85	14	53	18	12	4		1	
		1998	2	34	9	1	64	17		10	22	1		7	
	Spencer Gulf	Nth Spencer Gulf	1996	32	3	100		4			10		2		
			1997	77	4	115		2			7				
Port Lincoln		1995	122	14	131	12	2			3	2		6		
		1996	56	98	148	13	15			2	14		3		
		1997	34	28	35	2	6				3				
Port Rickaby		1996	3	31	38	9	3								
		1997	59	87	134	20	17		3						
Wardang Island		1997	9	153	29	9	73	29		17	26			4	
		1998	3	93	18	2	54	29		4	58			7	
West coast of Eyre Pen.		Denial Bay	1995	198	53	251	4	6			8		4		
			1996	94	59	155	1	10			8		4		
			1997	89	23	104	1	6			5		1		
	Streaky Bay	1995	150	19	155	4				3		3		3	
		1996	44	34	83	2	1			1		1		1	
		1997	24	35	29	5	5			3		2		2	
	Baird & Venus	1995	25		34										
		1996	110	11	133										
		1997	45		55										
	Coffin Bay	1995	91	7	100	2									
		1996	20	2	28										
		1997	37	12	70										

Off Wardang Island in the south-east, most ovary weights were between 10 – 40 g but ranged up to 80 g. Most males had developing testes, many of which were between 10 – 30 g (Fig. 4.2). Of the females 80.7% had developing ovaries. Mature fish were represented in all age

classes even the 3 year age class. A total of 58 fish were recognised macroscopically as having hydrated oocytes (Table 4.3), and further proof of spawning activity came from the 143 ovaries examined microscopically, of which 51.7% had post-ovulatory follicles (Table 4.3).

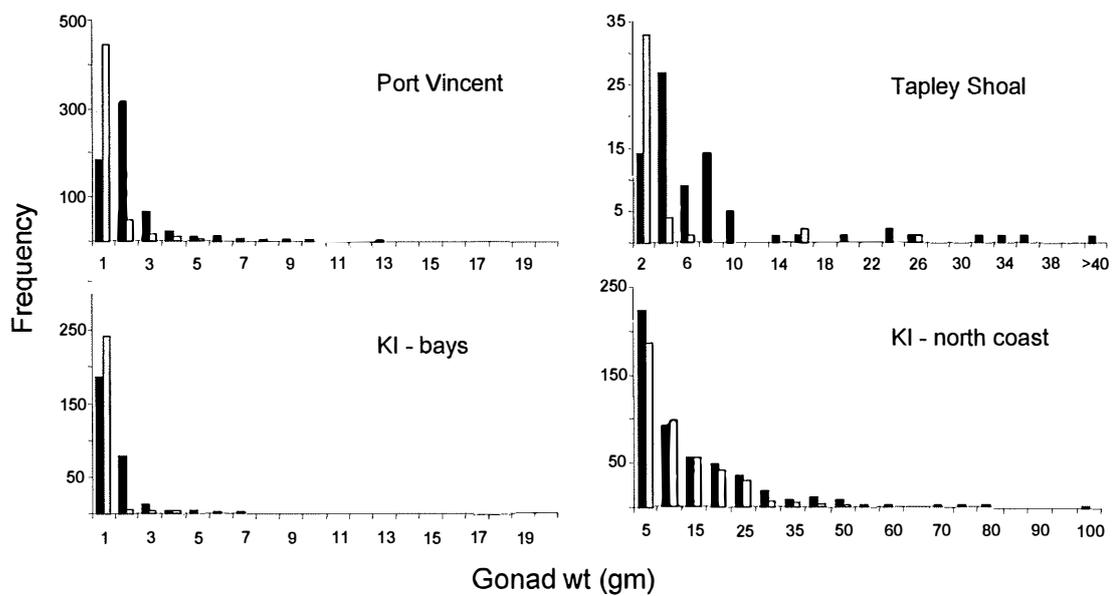


Fig. 4.1 Frequency distributions of gonad weights from King George whiting from four localities in the eastern region accumulated across years (shaded bars, females; light bars, males).

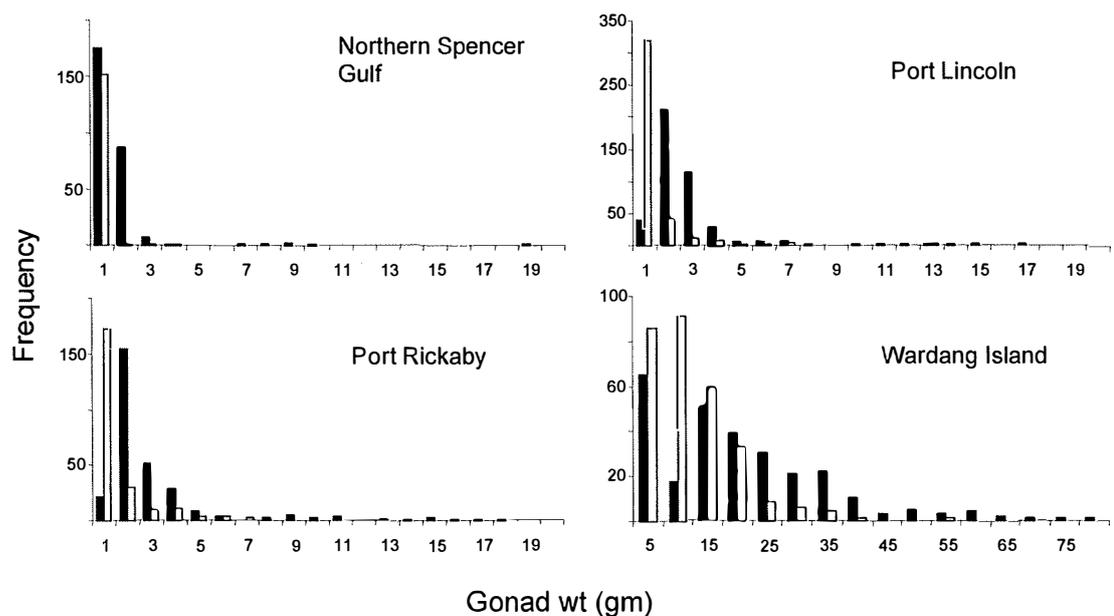


Fig. 4.2 Frequency distributions of gonad weights from King George whiting from four localities in the Spencer Gulf accumulated across years (shaded bars, females; light bars, males).

West Coast

There was no evidence of spawning activity in the samples from any west coast bay. Ovaries were generally small with the modal size around 1 – 1.4 g, and rarely exceeded 2 g. Testes generally weighed < 1 g (Fig. 4.3). At such localities only a small percentage of females showed any ovary development, that were classified up to macroscopic stage 3 (Table 4.3). Of 43 pairs of ovaries from the four localities examined microscopically none showed either hydrated oocytes or post-ovulatory follicles (Table 4.3). A higher percentage of males had developing gonads than the females (Table 4.3), but these generally showed only minimal development and none was ever running ripe.

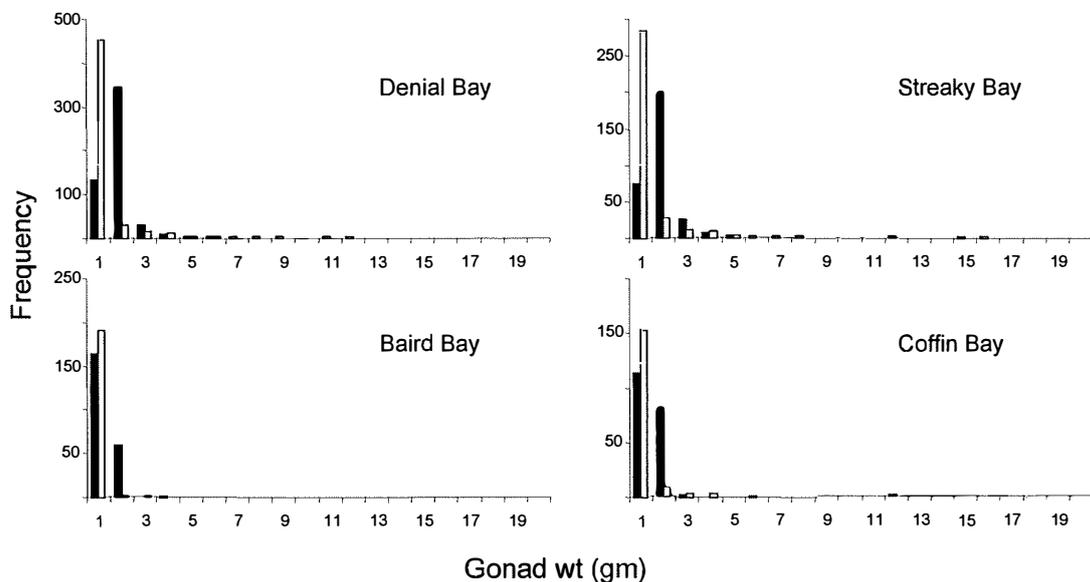


Fig. 4.3 Frequency distributions of gonad weights from King George whiting from four localities on the west coast accumulated across years (shaded bars, females; light bars, males).

Temporal Nature of Gonad Development

A total of 1,611 fish were collected between 1996 and 1998 from the north coast of Kangaroo Island and south-eastern Spencer Gulf (Table 4.4). These samples were examined in more detail to determine the reproductive mode, estimate spawning fractions and frequencies and batch fecundities, which are presented below.

Gonosomatic indices

Variation in gonosomatic indices indicated that the significant reproductive period included March to May, with the peak in April. In 1996, gonosomatic indices increased from March, peaked in April at 5-6% for both sexes, then decreased to May, and further to July (Fig. 4.4). The largest pairs of ovaries and testes were 72.1 and 43.5 g, respectively. At Kangaroo Island in 1997, gonosomatic indices increased weekly through March, with the largest ovaries at 97.3 g and testes 44 g. Unfortunately, no samples were obtained from then until late May, by which time the gonosomatic index had decreased substantially. In south-eastern Spencer Gulf gonosomatic indices from two samples collected in April were substantially higher than for the sample from March 1997 (Fig. 4.4).

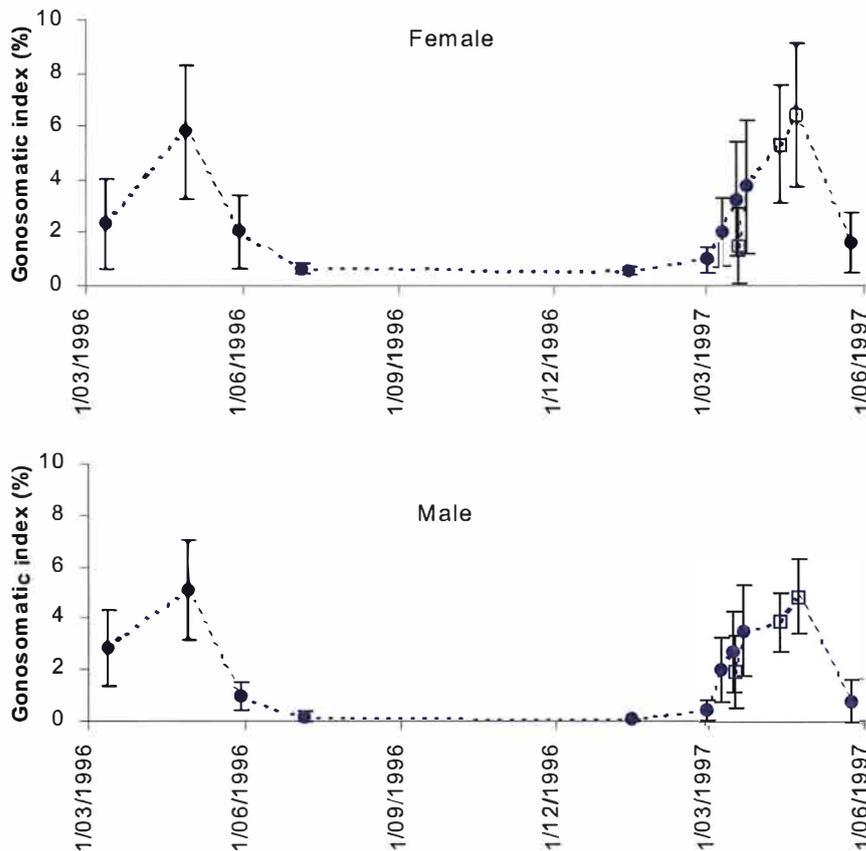


Fig. 4.4 Mean (\pm SD) gonosomatic indices for both sexes for each sampling occasion (circles from Kangaroo Island; squares from Wardang Island and Corny Point).

For females ($N = 32$) collected in April 1996, relationships between ovary weight (O_w) and ovary-free fish weight (W_f) were compared between fish classified at Stages 3 and 4 (Fig.

4.5). The two relationships respectively were: for Stage 3 $O_w = -1.9326 + 0.0434(W_f)$ ($r^2 = 0.507$, $p < 0.001$, $n = 17$); and for Stage 4 $O_w = -4.1904 + 0.0928(W_f)$ ($r^2 = 0.7886$, $p < 0.001$, $n = 15$). Comparing the lines suggests that ovaries more than doubled their weight through the hydration process. The mean (\pm SD) gonosomatic indices for the two samples were 3.77 (± 0.92)% and 8.16% (± 1.5)% respectively, representing an increase of 116.2% due to hydration.

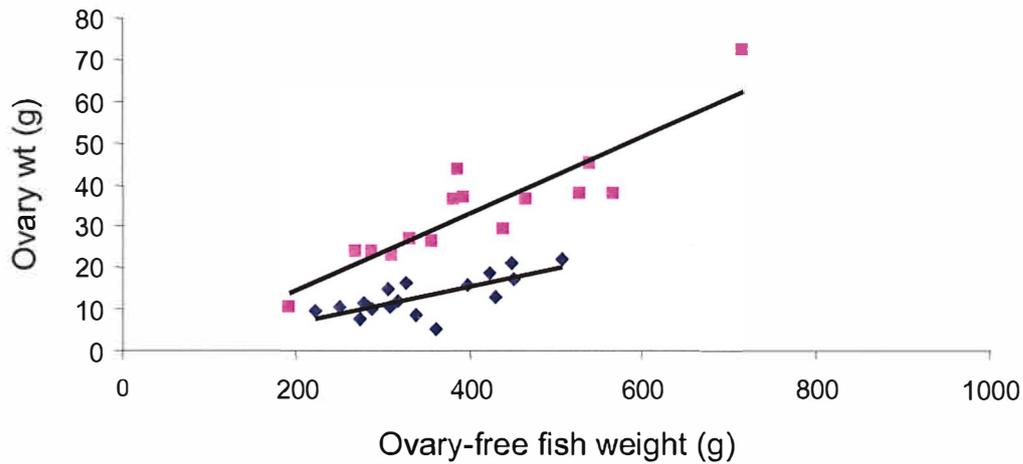


Fig. 4.5 Relationship between ovary weight and ovary-free fish weight for mature females ($n=32$) caught in April 1996 (diamonds, fish classified at macroscopic stage 3; squares for those at stage 4).

Table 4.4. Information on locality, date, mode of collection and results from the classification of development stages of gonads for each sample considered in the analysis of reproductive biology. Loc = Locality, KI = Kangaroo Island, WI = Wardang Island, CP = Corny Point; for mode of collection C = sub-sampled from commercial catch, P = purchased from commercial fishery, R = obtained from recreational fishers, S = caught on scientific cruise. For males data are the relative numbers of inactive (In) and developing (Dev) fish; for females the numbers classified to each macroscopic stage defined in Table 2, with the numbers examined histologically indicated in brackets.

Loc	Date	Mode of collection	N	Males		Females – macroscopic stage				
				In	Dev	1	2	3	4	5
KI	13/3/96	C	86	-	64	3	7 (1)	10 (10)	2 (2)	-
	30/4/96	C	100	-	68	-	-	17 (17)	15 (15)	-
	31/5/96	C	53	-	33	1	-	2 (2)	2 (2)	15 (1)
	6/7/96	R	89	8	6	47	-	-	-	28
	15/1/97	R	28	9	-	19 (4)	-	-	-	-
	2/3/97	C	52	3	15	19	13	2 (2)	-	-
	10/3/97	C	119	1	75	9	12 (1)	21 (15)	1 (1)	-
	18/3/97	C	59	-	35	2	2	18 (17)	2 (1)	-
	24/3/97	C	96	-	37	9	9 (1)	36 (22)	5 (5)	-
	25/5/97	C	120	11	28	24	-	9 (9)	5 (5)	43 (4)
	30/5/97	S	177	2	75	9	6	38	1	46
	4/5/98	C	127	2	34	9	1	64(64)	17(17)	-
WI	19/3/97	P	159	9	91	29	9	19 (14)	2 (1)	-
	14/4/97	P	95	-	47	-	-	35 (14)	13 (10)	-
CP	24/4/97	S	52	-	19	-	-	19 (17)	14 (13)	-
WI	17/4/98	C	91	3	44	14	1	16(15)	13(13)	-
	24/4/98	C	108	0	49	4	1	38(36)	16(14)	-

Macroscopic staging of ovaries

In March 1996 ovaries from fish collected off the north coast of Kangaroo Island, were classified to a range of macroscopic stages, although most were at Stages 2 and 3 (Table 4.4), indicating that ovary maturation was well advanced in some fish, but had not yet commenced in others. This diversity in development states was not apparent in late April when all 32 females were classified as developed (Stage 3) or gravid (Stage 4). By late May, most females were regressing (Stage 5), although a small percentage were still in active reproductive mode. By early July all ovaries were at Stages 1 or 5, indicating that the spawning season was complete.

Of the samples from Kangaroo Island in 1997, there was no sign of gonad maturation until early March (Table 4.4). By 10 March, most females were developing and over the following weeks the proportion of developed fish increased. By late May, a small proportion was still spawning but approximately 50% of ovaries were regressing. The diversity in development states was also apparent in the first sample from Wardang Island in March 1997 (Table 4.4).

By mid-April, all females from Wardang Island and Corny Point were developed or gravid. Most males had developing testes, particularly those caught in late April, and the samples collected some period after April had higher proportions of inactive males.

In 1998 sampling was concentrated in April and early May. The sample from Kangaroo Island consisted of 127 fish and most of the 91 females had well developed ovaries, 17 with hydrated oocytes (Table 4.4). Most developed females also had post-ovulatory follicles indicating they had spawned within the last day or so. From Wardang Island all males had developed testes whilst 82% of females had developing or developed ovaries. Twenty nine had hydrated oocytes and 74 had old post-ovulatory follicles. The estimates of spawning fraction suggest that >70% of females were in spawning mode at the time of capture.

Description and Interpretation of Microscopic Characteristics

Organisation and size of oocytes

The analysis of histological preparations revealed that oocytes at a range of developmental stages, and post-ovulatory follicles, could co-occur in developing and developed ovaries (Figs. 4.6, 4.7). In histological sections unyolked oocytes measured from 13 to > 100 μm in diameter, and overlapped in size with small partially yolked ones, which attained up to 260 μm and overlapped with small advanced yolked oocytes (Fig. 4.6). Although the preservation and histological processes are likely to have affected the sizes of oocytes, these data still demonstrate that size distributions were essentially continuous across developmental stages.

The size distributions of formalin-preserved oocytes were also complex, being either bimodal or trimodal with modes around 280, 380 and 530 μm (Fig. 4.7). Hydrating oocytes ranged from 750 to >1,000 μm , with the mode for fully hydrated ones around 900 μm . Thus, size distributions of oocytes were continuous between developmental stages, except for the clear gap that emerged when oocytes developed from the advanced yolked to the hydrating stage (Fig. 4.7).

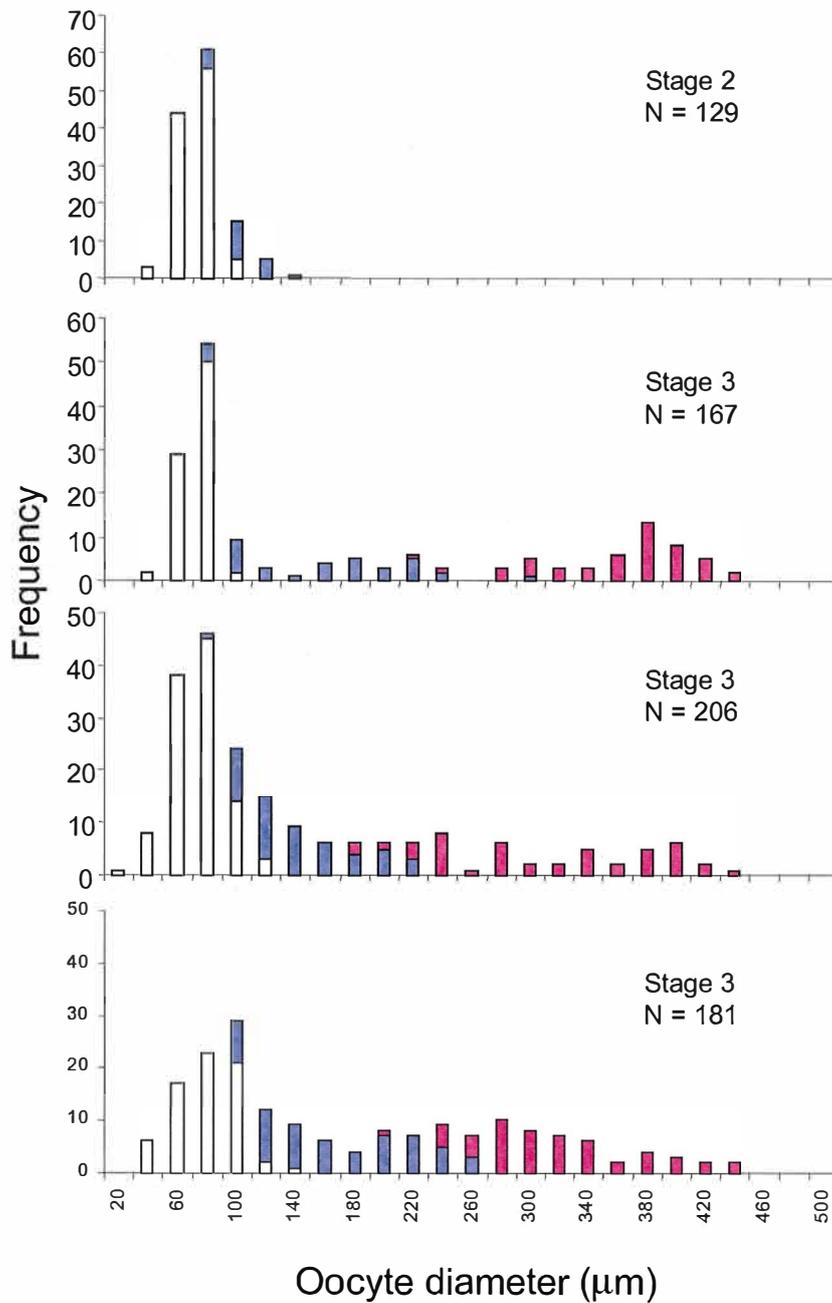


Fig. 4.6 Size frequency distributions of oocytes at different development stages, measured from histological sections of ovaries from fish classified to macroscopic stages 2 and 3. For the two lower graphs both fish had spawned only a few hours prior to capture (N, number of oocytes measured; bar colour represents type of oocyte: white, unyolked; grey, partially yolked; dark, advanced yolked oocytes).

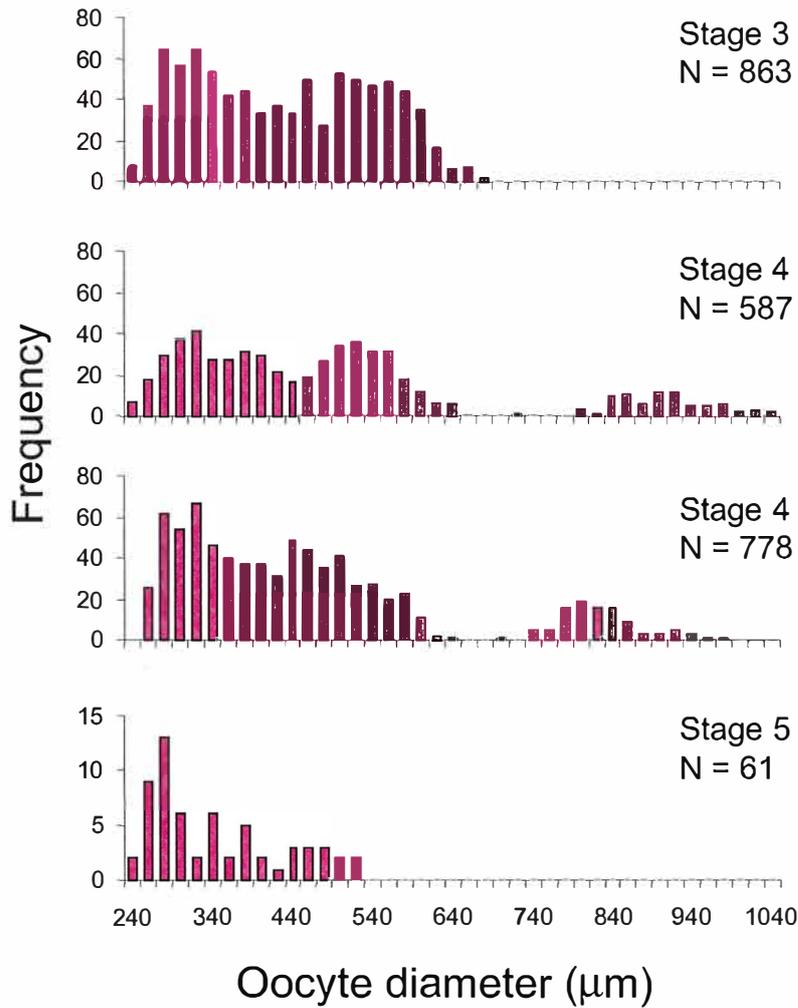


Fig. 4.7 Size frequency distributions of formalin-preserved whole oocytes from four fish classified to macroscopic stages 3, 4 or 5. The fish represented in the top graph had spawned only a few hours prior to capture (N, number of oocytes measured).

Time of day of spawning

For fish taken on one scientific cruise (Corny Point on 24 April 1997) the time of capture of each fish was recorded. Fishing was done at one site characterised by two large mounds at 40 m depth, located approximately 6 nm from shore. The fishing period was from 9.00 to 17.30 hours, during which time 19 males and 33 females were captured. Most females taken between 9.26 to 14.03 hours had hydrating oocytes and old post-ovulatory follicles (Table 4.5), indicating they were preparing to spawn, and probably had spawned one or several days earlier. Several ovaries also had new post-ovulatory follicles suggesting that ovulation had started.

Table 4.5. Relationship between time of capture of each female, the most advanced stage of oocyte development and the presence/absence of new and old post-ovulatory follicles, determined by histological analysis of ovaries for females caught at Corny Point on 24th April 1997.

Time of capture	Most advanced stage of oocyte development		Type of post-ovulatory follicles	
	Adv	Hyd	New	Old
9.26		+		+
9.32		+		+
9.42	+			+
9.52	+			+
10.01	+			+
10.05		+		+
10.05		+		+
10.47		+		+
10.48	+			+
11.05		+		+
11.13		+		+
11.13		+	+	+
11.55		+		+
12.26		+		+
12.50		+	+	
13.45		+		+
14.03		+		+
15.37	+			+
16.10		+	+	+
16.15	+		+	+
16.55	+		+	+
16.55	+		+	+
17.00	+		+	+
17.00	+		+	+
17.01	+		+	+
17.05	+		+	+
17.10	+		+	+
17.12	+		+	+
17.20	+		+	+

No fish were caught through the period of 14.03 to 15.33 hours. Of those taken after this time, one had hydrated oocytes, all of which were fully ovulated. The remainder had new post-ovulatory follicles, but no hydrated oocytes. These observations suggest that spawning occurred through the period of 14.03 to 15.33 hours. High tide was at 16.07 hours, so at the time of spawning, the tide was flooding and the current very strong. The drop in catch rate in the early afternoon may have been due to the spawning activity or to the difficulty of line-fishing in 40 m of water in a strong current.

Spawning fraction and frequency

Two methods based on histological analysis were employed to determine the spawning fraction. Despite some relatively minor differences in estimates from both techniques, there was an over-riding temporal trend regardless of sample site (Table 4.6). In March, the estimates of spawning fraction were generally low, but increased through the month. In April, the estimates were high, and on one occasion suggested that every female was spawning. By late May, spawning fraction had decreased to less than 20%, and in July 1996 no females were spawning.

The estimates of spawning fraction were used to estimate the mean spawning frequency through the periods encompassed by our sampling in both years. For the 80 day period of 13 March to 31 May 1996 the gonads from 70 mature females were examined, of which 35 were spawning at the time of capture (Table 4.6). This means that the fraction of females spawning per day was $35/70$ (i.e. 0.5), equating to each female spawning on average once every 2 days. Consequently, over the 80 day period females spawned an average of 40 times.

Using all data from 10 March to 25 May 1997 (77 days), the ovaries of 289 mature females were examined (Table 4.6). Of these, the first method for estimating spawning fraction identified 80 spawning females, equating to a female spawning on average once every 3.6 days, i.e. 21 spawnings through the 77 day period. Alternatively, the second method for estimating spawning fraction identified that 103 fish were spawning, equating to females spawning on average once every 2.8 days, i.e. 27 spawning events over the 77 day period. There were time-series data available for 1998, and so spawning frequency could not be estimated.

Table 4.6. Estimates of spawning fraction for each sample of fish. The two estimates of spawning fraction were based on the proportion of mature females (Stages 2-5) that either would have spawned on the day of capture or had spawned prior to the day of capture.

Loc	Sample date	No. females	No. mature females	No. spawning on day of capture	Spawning fraction	No. spawned prior to day of capture	Spawning fraction
KI	13/3/96	22	19	3	0.158	1	0.053
	30/4/96	32	32	31	0.969	32	1.0
	31/5/96	20	19	2	0.105	2	0.105
	6/7/96	75	28	0	0	0	0
	15/1/97	19	0	0	0	0	0
	2/3/97	34	15	0	0	0	0
	10/3/97	43	34	3	0.088	3	0.088
	18/3/97	24	22	7	0.318	2	0.091
	24/3/97	59	50	10	0.2	13	0.26
	25/5/97	81	57	12	0.211	11	0.193
	4/5/98	91	82	23	0.296	69	0.864
W1	19/3/97	59	30	2	0.067	4	0.133
	14/4/97	48	48	20	0.417	38	0.792
CP	24/4/97	33	33	26	0.788	32	0.970
W1	17/4/98	44	30	19	0.71	25	0.93
	24/4/98	59	55	39	0.798	49	0.998

Relationships between batch fecundity and fish size and age

At Kangaroo Island the relationships between the number of hydrated oocytes in the ovary and TL were compared between 1996 and 1997 using analysis of covariance, and found not to differ between years (F-ratio for slopes = 0.0585, $p = 0.8109$; F for intercepts = 0.9308, $p = 0.3435$). A similar result was obtained for the relationship between batch fecundity (BF) and W_f (F for slopes = 0.6803, $p = 0.4143$; F for intercepts = 0.2968, $p = 0.5905$). Consequently, the data were pooled across years, and linear regressions used to describe relationships between BF with TL, W_f and fish age (Fig. 4.8, Table 4.7). Significant relationships explained 45.7 and 62.9% of the total variation in numbers of hydrated oocytes respectively (Fig. 4.8, Table 4.7). The relationship between BF and age was not significant at the 5% significance level.

The data from Wardang Island and Corny Point in 1997 were pooled and linear relationships determined, and were stronger than those for Kangaroo Island explaining a higher percentage of the variation in BF (Table 4.7). These relationships were compared with those for Kangaroo Island identifying highly significant differences between localities. Fish from south-eastern Spencer Gulf had a substantially higher batch fecundity than did similar-sized fish from Kangaroo Island (Table 4.7).

Table 4.7. Results from regression analyses between batch fecundity (BF) and fish size (TL), ovary-free weight (W_f) and age for samples from Kangaroo Island combined from 1996 and 1997 [KI('96 + '97)], and combined samples from Wardang Island and Corny Point [WI + CP('97)]. Columns 6-9 show results of analyses of covariance between regression lines for the two localities. ** = significant at $p = 0.01$, ns = not significant at $p = 0.05$. Analysis of covariance not done for BF and age because of the non-significant relationship at $p = 0.05$.

Samples	Equation	N	r^2	P	Factor	df	F-ratio	P
KI ('96 + '97)	BF = 461.16(TL) - 143,772.8	29	0.4567	0**	Slopes	1,53	8.9099	0.0043**
WI + CP ('97)	BF = 936.47(TL) - 314,617.2	28	0.6779	0**	Intercepts	1,54	16.1586	0.0002**
KI ('96 + '97)	BF = 129.07(W_f) - 10,254.66	29	0.6285	0**	Slopes	1, 53	11,3192	0.0014**
WI + CP ('97)	BF = 263.29(W_f) - 39,334.9	28	0.6570	0**	Intercepts	1,54	22.3256	0**
KI ('96 + '97)	BF = 3,731.1(Age) - 24,202.65	29	0.0935	0.0589 ns				
WI + CP ('97)	BF = 21,554.7(Age) - 30,872.3	28	0.484	0**				

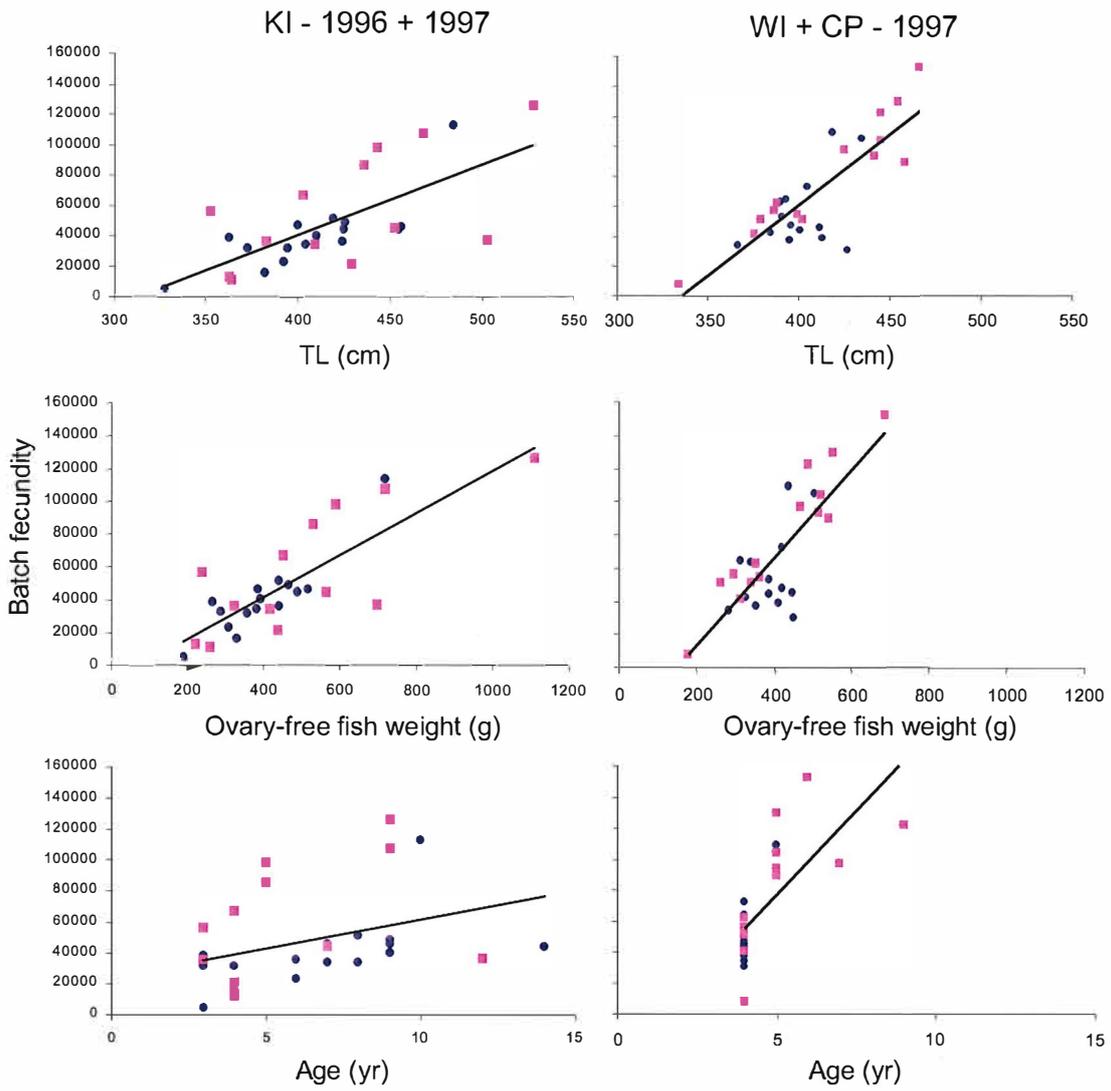


Fig. 4.8 Relationships between batch fecundity and fish size, weight and age. Left hand graphs represent samples from Kangaroo Island combined between 1996 and 1997, right hand graphs for samples from Wardang Island and Corny Point in 1997 (closed circles, fish sampled in 1996; closed squares, fish sampled in 1997).

4.4 Discussion

Geographic Variation in Gonad Development

There was considerable spatial variation in the extent to which gonads developed and where this eventually culminated in spawning activity. We have determined that there was a complex interaction between population structure, reproductive maturation and habitat. Populations dominated by young fish generally had at least a few individuals whose gonads showed some development. Although a few such females developed large, distended ovaries full of advanced yolked oocytes, none ever showed evidence of spawning. That some ovaries were regressing, suggests that oocytes progressed directly from the advanced yolked stage to α -atresia, by-passing hydration and spawning. Such a phenomenon has previously been described for the ovaries of southern bluefin tuna (*Thunnus maccoyii*). Those fish captured away from the spawning grounds displayed some ovary maturation and oocyte atresia but no evidence of spawning (Farley and Davis 1998).

Even in southern Spencer Gulf many 4 and 5 year old King George whiting had highly developed gonads, but did not show no evidence of spawning activity. The few localities where gonad maturation resulted in spawning, i.e. in the region of Investigator Strait (Tapley Shoal and Kangaroo Island), and off-shore in south-eastern Spencer Gulf, were those with the broadest age and size ranges (Chpt 3). At such places most fish became mature and spawned despite many being smaller and younger than non-spawning fish at other localities. This suggests the influence of two possible cues on the success of reproductive maturation: the presence of older, mature fish; or the effect of the exposed nature, deep water and reef habitat that is typical of the spawning grounds.

Our analysis of gonads has revealed that fish as young as 3 years and small as 320 mm TL, can mature and spawn. Yet, relative to the pattern of dispersion of adult fish, the location of spawning grounds is extremely limited, as was also described for Western Australian populations (Hyndes et al. 1998). In South Australia this corresponds to the patterns of distribution and abundance of eggs and larvae of King George whiting throughout Gulf St. Vincent, Spencer Gulf and Investigator Strait that were identified by plankton surveys between 1986 and 1991. Such surveys showed the highest abundances of larvae were in Investigator Strait and southern Spencer Gulf compared with the northern parts of both gulfs. Furthermore, larvae less than 10 days old were found only in lower Spencer Gulf and Investigator Strait with older, larger ones caught further north (Bruce pers. comm.).

Gonad maturation and spawning

Gonad maturation of King George whiting in South Australia occurred at least from early March until late May, with the peak spawning time through the latter part of April. This timing differs from that at other places across southern Australia. Recruitment to Victorian nursery areas resulted from spawning that occurred from mid-April to mid-July peaking through mid-May to early July (Jenkins and May 1994), approximately one month after the peak in South Australia. Along the south-western coast of Western Australia spawning starts in June and continues until September (Hyndes *et al.* 1996). Such large-scale spatial differences may relate to different seasonal water temperature regimes (Hyndes *et al.* 1998). The south-flowing Leeuwin Current brings warm tropical waters down the coast of Western Australia, resulting in a slow seasonal decline in water temperature in the south west to 17-19°C between June and September (Hyndes and Potter 1996). However, in the region where this study was done there is no tropical thermodynamic influence and the water temperatures drop quickly from around 23°C in summer to 17-19°C between March and June (Fowler unpublished data).

Reproductive mode

The relative frequencies of oocytes at different development stages can be indicative of the reproductive mode for a species of fish (Hunter and Macewicz 1985; Davis and West 1993; Hunter *et al.* 1992; Cuellar *et al.* 1996; Farley and Davis 1998). Such studies have shown that the characteristics that typically distinguish indeterminate from determinate fecundity are: oocytes usually co-occur in all development stages; they range in size continuously from small to the advanced yolked stage; and there is no large hiatus between maturity classes of oocytes, except that between hydrated and advanced yolked oocytes. The ovaries of King George whiting demonstrated all such characteristics, suggesting that oocytes develop from the unyolked stage, through vitellogenesis to hydration throughout the spawning period of each fish. As such, the data suggest that annual fecundity is indeterminate, i.e. not fixed prior to the on-set of the spawning season.

The size distributions of oocytes at different stages of development also indicated that only a subset and not all advanced yolked ones became hydrated and were released on one occasion. This, in association with the simultaneous presence of different stages of development, indicates that oocyte development was asynchronous, i.e. all maturing oocytes did not undergo vitellogenesis simultaneously (Wallace and Selman 1981; West 1990). Furthermore,

the co-occurrence of hydrated oocytes and post-ovulatory follicles indicates that females spawned several times, if not over consecutive days, at least within a few days of each other. These features indicate the high likelihood that this species is a multiple batch spawner with asynchronous development and indeterminate fecundity.

Estimation of Spawning Fraction and Frequency

Here, two methods were used to estimate spawning fraction based on the principle of determining the proportion of mature females that had or would spawn on a particular day (Hunter and Macewicz 1985). The first method identified those fish that did or had spawned on the day of fish capture. Unlike the “hydrated oocyte” method (de Martini and Fountain 1981; Hunter and Macewicz 1985), where impending spawners caught at a particular time of day were identified by gross examination of ovaries, we based this analysis on the histological examination of ovaries. We included all fish that showed indications that spawning had, or still would take place on the day of capture, including; migratory nucleus oocytes, hydrated oocytes and new post-ovulatory follicles. By so doing, this method accommodates the various changes in oocyte and ovary characteristics that occur through the day on which a fish spawns.

The second method for estimating spawning fraction was the “post-ovulatory follicle” method (Hunter and Macewicz 1985). Despite the general consistency of the results between this and the previous method, this was more problematical to apply for our samples. Firstly, the histological preparations from many ovaries with hydrated oocytes did not section well, resulting in the arrangement of oocytes, post-ovulatory follicles and ovary matrix being disrupted. Such poor histological sections may have resulted from the delay between fish capture and ovary preservation for the samples collected from the commercial fishery. The second problem here was that although we only distinguished two age classes of post-ovulatory follicles, those we classified as old may not have necessarily related to a single spawning event, but to spawning events over several days. The degeneration of post-ovulatory follicles is a species-specific and temperature-dependent phenomenon that may well take more than 24 hours (Hunter and Macewicz 1985; Fitzhugh and Hettler 1995). For the King George whiting the most tractable method for determining the time required for degeneration of post-ovulatory follicles would be experimental, where tank-maintained brood stock were induced to spawn, and were then sampled at pre-determined intervals after spawning, for analysis of the structure of post-ovulatory follicles (Fitzhugh and Hettler 1995).

Estimates of spawning fraction from both techniques conformed to the same seasonal reproductive pattern that has already been established, i.e. the proportion spawning in March was low, increased and peaked in April and subsequently declined. The peak spawning fraction of near 1.0 in late April converts to a spawning frequency of most females spawning every day. Unfortunately, our restricted sampling prevented us from determining over what period this high frequency of spawning was sustained.

Many other temperate and tropical species have indeterminate fecundity (Hunter *et al.* 1985), and they typically spawn numerous times through a reproductive season (de Martini and Fountain 1981; Hunter *et al.* 1985; Davis and West 1993; Farley and Davis 1998). Although for the King George whiting the spawning frequency varied through the season, the average rates for the periods during which we sampled in both 1996 and 1997 ranged from one spawning every 2 days to one every 3.6 days. Although these estimates should only be considered preliminary because of our limited sampling, nevertheless they provide the first evidence that female King George whiting spawn at least 20 times, if not many more times, throughout one spawning season.

Relationship between gonad maturation with fish size and age

We intended to determine the L_{50} and minimum age of reproductive maturity for King George whiting. However, it was found that such concepts did not really apply here, since all size and age classes sampled were reproductively active. The small number of individuals that were not reproductively active, were taken at either end of the reproductive season and would likely have matured at some time through the season.

The reason for the lack of small, non-reproductive fish in both localities is evident from tag-recapture data for King George whiting in South Australia (Chpt 6, Jones *et al.* 1990; Fowler and McGarvey 1997). Such analyses have demonstrated that fish around the ages of 3 – 4 years, move up to several hundred kilometres from shallow, inshore, coastal areas and accumulate in such deep, off-shore, exposed locations as the sample sites where spawning occurred. Fish generally exceeded the minimum legal size of 30 cm TL when such movements were made. The extended age distributions at the spawning areas suggest that fish remain in such places for extensive periods, if not the remainder of their lives.

Relationships between batch fecundity and fish size and age

Batch fecundity was estimated as the number of oocytes that became hydrated on the day that a fish was caught, and here ranged between 5,250 to 152,191 depending on fish size. The differences amongst fish were more closely related to fish weight than to length, which is typical for teleost fishes (Nikolskii 1969). The rate of egg production, however, did not vary with fish weight, suggesting that for King George whiting both small and large females allocated proportionally similar energy levels to egg production. In this sense our results contrast with those for other fish species (de Martini and Fountain 1981; Hunter and Macewicz 1985). However, the comparison of fecundities between Kangaroo Island and south-eastern Spencer Gulf did indicate substantial spatial variation in the rate of egg production for similar sized fish, which must reflect a substantial habitat effect between the two localities.

For fish species with indeterminate fecundity the annual fecundity is a function of batch fecundity and spawning frequency (Hunter and Macewicz 1985; Davis and West 1993; Farley and Davis 1998). Here we can provide preliminary estimates of annual fecundity based on the ranges in our estimates of batch fecundity (5,250 – 152,191) and spawning frequency (21 – 40 spawnings). By multiplication, annual fecundity ranged from 110,250 to 6,087,640 eggs depending on fish size. Earlier estimates of fecundity for King George whiting ranged from 100,000 to 800,000 eggs depending on fish size (Cockrum and Jones 1992), but these were based on counts of oocytes >300 µm in diameter, which relate to our advanced yolked oocytes. We now know that the standing crop of such oocytes is synonymous neither with the number that would become hydrated on a particular day, nor the number that would be released over an entire spawning season.

4.5 References

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CHAPTER 5. RECRUITMENT AND EARLY LIFE-HISTORY

A.J. Fowler

5.1 Introduction

In Chapter 3 we determined that adult King George whiting are not dispersed evenly throughout the coastal areas of South Australia with respect to size and age. In Chapter 4 it was made apparent that adult fish are not reproductively active across their entire distribution but spawn at particular locations. We also know that the nursery areas to which post-larvae recruit are located in shallow, protected inshore waterways, particularly the large embayments and estuarine systems that support seagrass beds (Jones et al. 1990, Fowler and Short 1996, Fowler et al. 2000). The most important nursery areas are located in the northern parts of both gulfs, the north-eastern bays of Kangaroo Island and the west coast bays. Such nursery areas may be up to several hundred kilometres from the spawning grounds.

This chapter is concerned with the process of recruitment to nursery areas. Characteristically recruitment rates of marine species vary substantially in both space and time, reflecting influences that operate both before and immediately after settlement (Underwood and Fairweather 1989, Sale 1990). The former include the effect of variable ocean currents on larval transport, whilst the latter include habitat selection at settlement and post-settlement mortality. Such recruitment variability can directly influence population dynamics and demography (Doherty and Fowler 1994), and ultimately determine the size of fishery catches several years later, thus having profound economic implications (Jones and Dimmlich submitted). Therefore, estimates of recruitment rates are useful because they may help predict future trends in fishery catch, and indicate problem areas in the fishery.

Another important question that relates to the early life-history of fishes is the size of stock units. Most populations of finfish are divisible into numerous sub-populations that are self-recruiting and have little connection with adjacent groups (King 1995, Bailey 1997). The size of stock units may well be determined by the location of spawning grounds at which the recruits to adjacent areas originate. This relationship between spawning grounds and nursery areas concerns the duration of the larval phase and the geographic extent of larval advection. The size of such stock units sets the spatial scale at which population biology studies should be done, and the scale at which their fisheries should be managed.

In this study our aim was to determine the pattern of temporal variation in recruitment at several spatial scales and to determine whether there was any spatial coherence in these patterns. This would

provide some indication of the spatial scale over which the processes that regulate recruitment operate, which would assist in the determination of the size of stock units. Towards this secondary aim we also described early life-history characteristics for some of the sites where recruitment was being monitored. This was done on the basis that if post-larvae in different nursery areas originated from the same spawning grounds the timing of recruitment, timing of spawning, and early life-history characteristics would be similar. Alternatively, if they were dissimilar would suggest that post-larvae from different sites had originated from different places and independent spawning events.

The recruitment patterns of post-larvae to nursery areas were monitored on a monthly basis through the recruitment seasons of 1995 to 1997, whilst the early life-history characteristics at each site were explored through the interpretation of microstructure of otoliths from selected post-larvae from four sites that were located up to 500 km apart, that had been collected through 1994.

5.2 Materials and Methods

Sampling regime

Recruitment of King George whiting is here defined as the number of post-larvae caught in nursery areas. Some sampling was done prior to 1995 which served to choose sampling localities and sites on the basis of supporting shallow sub-tidal beds of seagrass (*Zostera* and *Heterozostera* spp.), and were firm underfoot for towing a net. The preliminary work also indicated that recruitment in South Australia occurred between June and November peaking through the period of late August to October (Fowler and Short 1996, Fowler et al. 2000). Consequently, for the years 1995-1997 sampling was done monthly between July and October – the period when recruitment was highest.

Sampling was done according to a hierarchical regime that incorporated several spatial scales: localities (10-100's km); places (km); sites (10's of metres); transects (metres). The hierarchy of sampling sites is shown in Fig. 5.1. In the Barker Inlet/ Port River system two places were each sampled at two sites (BI-1, BI-2, PR-1 and PR-2). Both of Franklin Harbor and Coffin Bay were sampled at an eastern and western place, with two sites at each place (Fig. 5.1). On the Far West Coast Streaky Bay, Acramen Creek and Davenport Creek were also sampled at two sites. At each place an area of 600m² was sampled on each occasion based on a regime of 3 transects of 40 m length and 5 m width. Sampling involved dragging a small beach seine net over the transect distance by two people, after which it was bundled up, and carried to the beach where the contents were sorted. Post-larval King George whiting were removed, counted and preserved in 70% alcohol. The net had a semicircular perimeter of 7 m, a mouth of 5 m, a drop of 2 m and a mesh size of 1 mm, and was held upright in the water column by a float and a lead line.

The catches of recruits were compared amongst months, places and sites for each locality using an analysis of variance. Also, the results for each year were used to calculate a recruitment index, which was the mean number of fish caught per transect from the catches in August, September and October (only September and October in Franklin Harbour), the months when the highest catches were made. From these annual means (\bar{x}_a) an overall mean (\bar{X}_a) across all years was calculated for each beach. The % deviation of each annual mean from the overall mean was calculated as: $D = (\bar{x}_a - \bar{X}_a) / (\bar{X}_a)$ %. These annual deviations were plotted against years for each site. Also, an annual mean for each locality was calculated from all the sites (\bar{X}_s). The % deviation of each site mean from this overall mean was calculated and plotted against year.

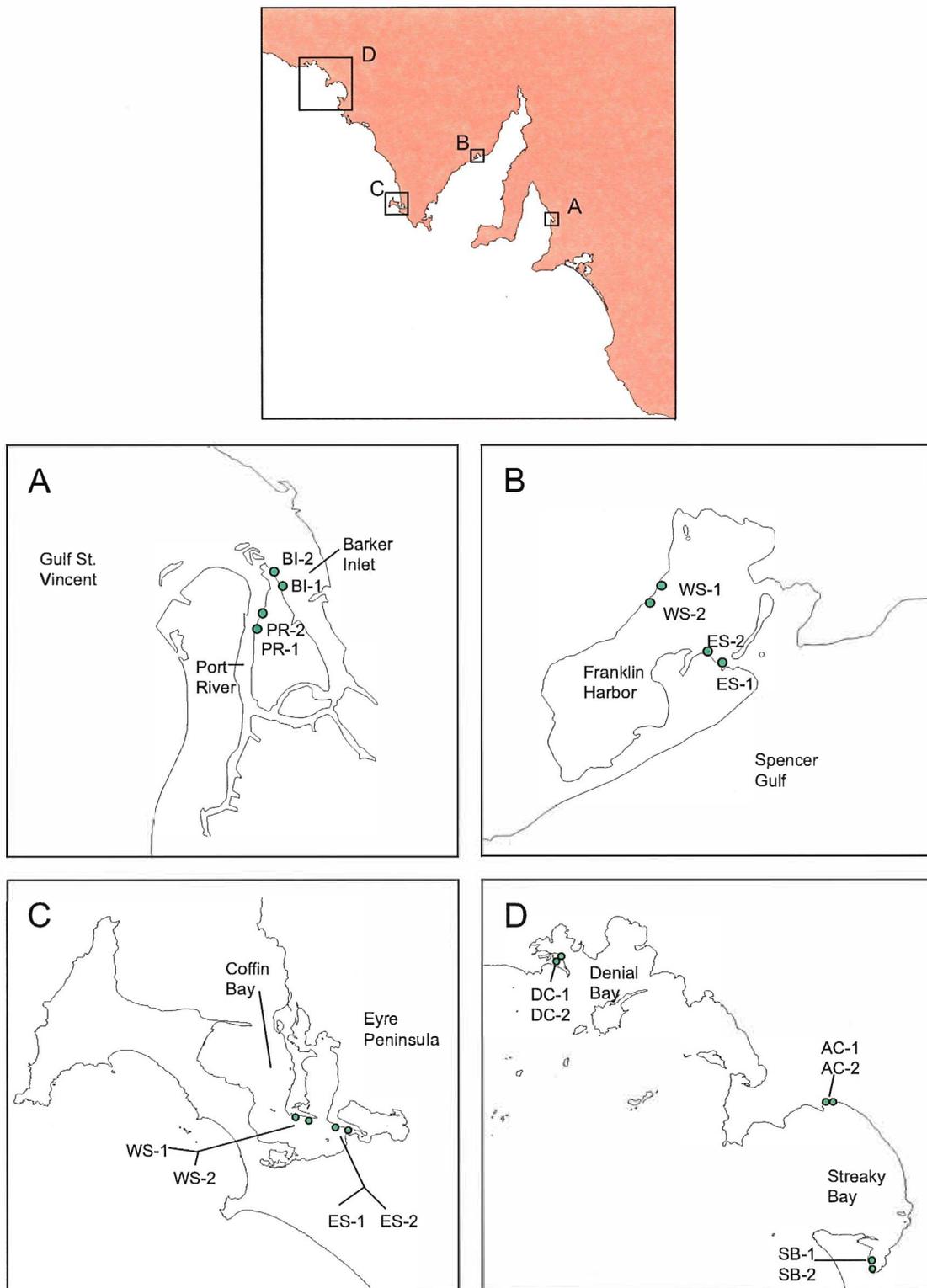


Fig. 5.1 Top map shows the map of South Australia, indicating the four localities where recruitment was monitored. Maps A to D show the four localities in detail, indicating the two places (three in Map D) and sites within places sampled at each locality.

Because our sampling gear was non-selective for fish size, the catch from each transect included a size range of post-larvae that would have settled at different times. As such, the size structures of catches were developed to help elucidate the temporal nature of the arrival of recruits into the nursery area. Post-larvae were measured to standard length (SL) to the nearest 0.1 mm using Vernier calipers. Fish from all three transects were measured. When their combined total exceeded 200 individuals, only a random sub-sample of this number was measured. Size structures were used as a qualitative indicator of recent recruitment. Hamer and Jenkins (1996) determined that the maximum size of pre-settlement King George whiting is 20.5 mm SL, and used the number less than this size as an index of recent recruitment. We, adopted the same protocol and divided the total number of fish from each sample into the proportion that were “small” (i.e. < 20.5 mm SL), and “large” (i.e. =>20.5 mm SL).

Post-larval ageing work

The four localities considered in this recruitment survey were also sampled in a pilot study in 1994. The post-larval ageing work was done for some of these fish collected in 1994. For three sampling occasions, i.e. July, September and October the 30 smallest post-larvae from each locality were selected for ageing on the assumption that they had settled most recently. These fish were measured and their sagittae removed under a binocular microscope. One sagitta was fixed with Super Glue to a microscope slide with the sulcus face upwards, and then ground and polished to the primordium using two grades of lapping film (9µm and 3µm). With the image of the otolith displayed on a video screen using an image analysis system, the otolith increments were counted from the anterior tip to the primordium. Two successive counts were made for one sagitta from each fish. When these differed by <5% their mean was used as an estimate of the number of increments, but when they exceeded this difference further counts were made until a satisfactory count was achieved, or the otolith was rejected. Because the first increment forms with first-feeding approximately 5 days after hatching (Bruce and Short, unpublished), post-larval age was estimated by adding five to the otolith count. These estimates of age were used to determine the dates on which fish were spawned, from which we constructed frequency distributions of spawning dates. Since the otoliths of King George whiting from South Australia do not display a distinct settlement mark it was not possible to divide microincrements into those relatable to the pre- and post-recruitment life-history stages.

5.3 Results

Comparison of recruitment rates

Barker Inlet / Port River

On each occasion we caught post-larvae at the four sites, with the highest catch of 1,012 post-larvae 200m^{-2} (Fig. 5.2). The catch rates varied significantly at two temporal scales, i.e. between months and years (Fig. 5.2, Table 5.1). Catches were always low in July, high in October, whilst those of August and September varied amongst years and sites. The significant year x month interaction (Table 5.1), may relate to the high catches in August 1996, and the low August catches of 1995 and 1997. With regard inter-annual variation, catches were generally higher in 1997, lower in 1996 and lowest in 1995 (Fig. 5.2). Only at BI-2 were catch rates not highest in 1997 (Fig. 5.2).

The spatial distribution of recruits also demonstrated significant variability both between places and amongst sites. In 1995 the Port River received higher recruitment than Barker Inlet (Fig. 5.3). However, in both 1996 and 1997 PR-1 received the highest overall recruitment whilst PR-2 was close to the lowest, even though these were separated by only several hundred metres.

In general, the proportion of the catch that was composed of small fish (<20.5 mm SL) decreased sequentially between July and October (Fig. 5.2). The size structures of catches in both 1995 and 1996 indicate that in July the catch comprised mainly small fish (Fig. 5.4). In the latter months it consisted of both small and larger post-larvae, indicating that the catch was comprised of both recent and earlier recruits (Fig. 5.4). Overall few fish less than 17 mm SL were ever captured. There were large numbers of small fish taken in September and October indicating that this was the main recruitment period.

Franklin Harbour

Recruitment to the 4 sites in Franklin Harbor varied significantly amongst months, but were consistent between years (Fig. 5.5, Table 5.2). Numbers of post-larvae were always low in July and August, and then substantially higher in both September and October. There was no consistent pattern of inter-annual variation amongst the four sites (Fig. 5.5).

The number of recruits differed significantly between places. The eastern place was closest to the entrance of the harbour and received the highest recruitment, although with considerable variation between the two sites (Fig. 5.6). The western place, located across the harbour from the entrance, always received substantially lower input rates.

In July and August there were few post-larvae present. In September, when numbers were higher, most post-larvae were small, indicating that this is an important recruitment period (Figs. 5.5, 5.7). Size structures in October consisted of both small and large fish indicative of recent and earlier recruitment. These size structures were not as broad as those from Barker Inlet, and indicated that the fish were generally smaller.

Coffin Bay

Recruitment to the 4 sites in Coffin Bay varied significantly amongst months but displayed no significant inter-annual variation (Fig. 5.8, Table 5.3). Generally, few post-larvae were present in July, whilst by August good recruitment had usually occurred at both sites at the western place. In general, highest catches were recorded at both places in September and October. There was no consistent inter-annual variation amongst the four sites (Fig. 5.8).

The pattern of distribution of post-larvae amongst the four sites was consistent and reflected the distance from the site to the entrance of the bay (Fig. 5.9). Recruitment was always highest at both sites at the western place, with much lower catches at the eastern place, where catches decreased away from the entrance to the bay.

The post-larvae caught in Coffin Bay were generally the smallest of all localities sampled (Fig. 5.10). Some as small as 13 mm SL were captured, whilst modal sizes of 15 – 16 mm SL were recorded. Only by October in each year were larger post-larvae captured.

Far West Coast (Streaky Bay, Acramen Creek, Davenport Creek)

Recruitment to the three west coast places demonstrated substantial variability at each level in the sampling hierarchy (Fig. 5.11, Table 5.4). Recruitment varied amongst months and years and the year x month interaction reflected the unpredictable nature of the catch in each August. This was generally consistent amongst the different places despite the significant month x place interaction. The pattern of variation from month to month was not consistent at the different places. Furthermore, the year x place interaction reflects that the pattern of variation at each place varied between years in different ways. In general, 1996 was the highest recruitment year, with the relative rates for 1995 and 1997 varying between places (Fig. 5.11).

The spatial distribution of recruits showed some consistency amongst years (Fig. 5.12). Streaky Bay tended to receive the highest recruitment, Acramen Creek and DC-1 at Davenport Creek received intermediate levels whilst DC-2 received the lowest.

The catches in July, August and September generally consisted of small fish with a modal size of approximately 16 – 17 mm SL (Fig. 5.13). Also, larger fish were captured in October reflecting recruitment over the previous couple of months.

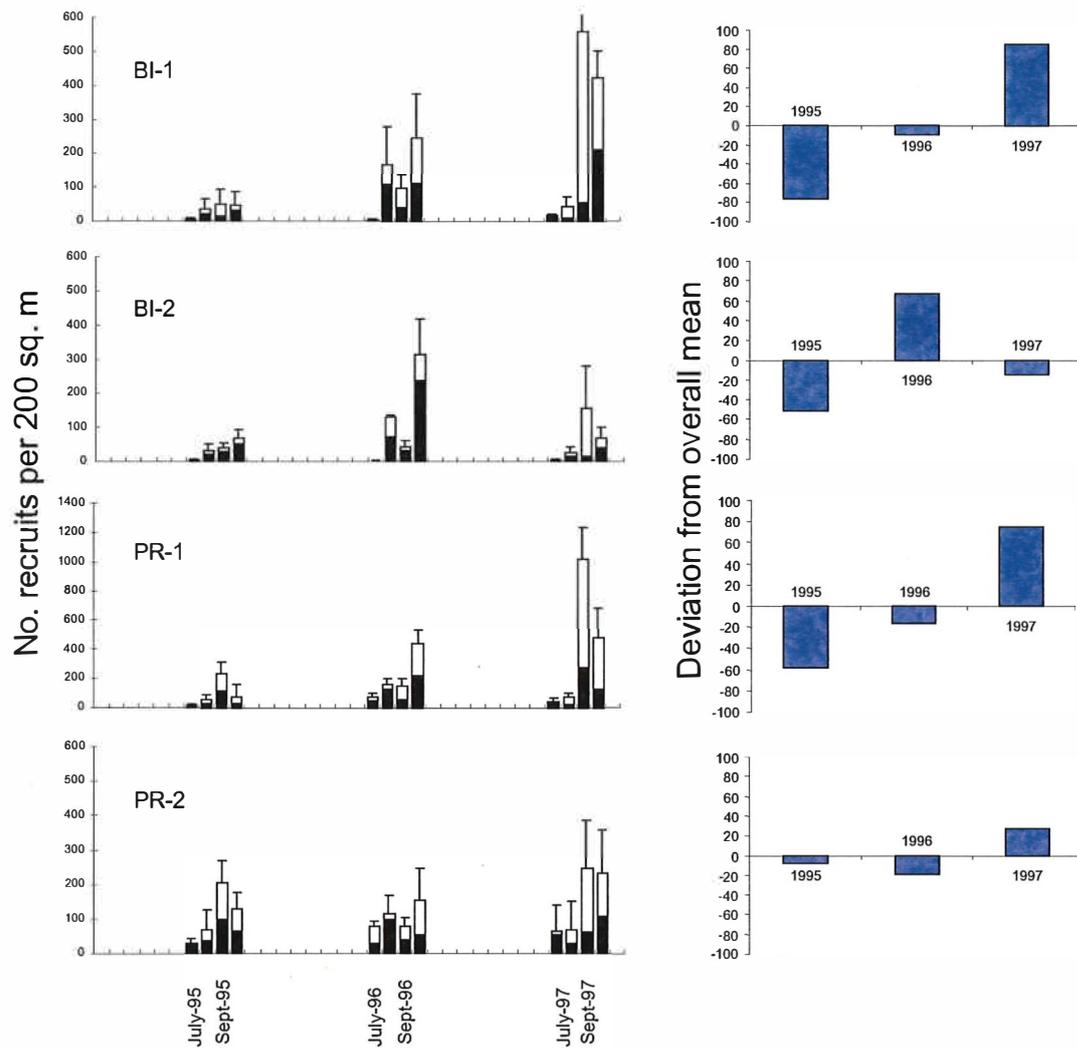


Fig. 5.2 Barker Inlet / Port River. Left hand graphs show the catch rates from recruitment sampling on each sampling occasion at each site between 1995 and 1997. The numbers are divided by size - shaded bars for fish <20.5 mm SL, light bars for fish >20.5 SL. Right hand graphs show the deviation of the annual mean for each site from the overall mean for that site calculated across the three years.

Table 5.1 Results of the analysis of variance on the monthly recruitment counts recorded in the Barker Inlet / Port River at the two sites within each place between 1995 and 1997. Prior to analysis the data were transformed using the square root transformation because of heterogeneous variances in the original data.

Factor	SS	Df	MS	F-ratio	probability
Year	564.147	2	282.074	5.9343	0.0081**
Month	2191.9	3	730.634	15.3711	0.0000**
Place	365.808	1	365.808	7.6959	0.0105**
Site	1140.79	24	47.533	5.3958	0.0000**
Year x Month	1020.71	6	170.119	3.5790	0.0112**
Year x Place	29.4322	2	14.7161	0.3096	0.7366
Month x Place	103.648	3	34.5495	0.7269	0.5460
Year x Month x Place	72.2363	6	12.0394	0.2533	0.9531
Residual	845.6805	96	8.8092		
Total	6334.3568	143			

Fig. 5.3 Barker Inlet / Port River. Graphs show the deviation of the annual mean for each site from the overall mean calculated across the four sites in each year.

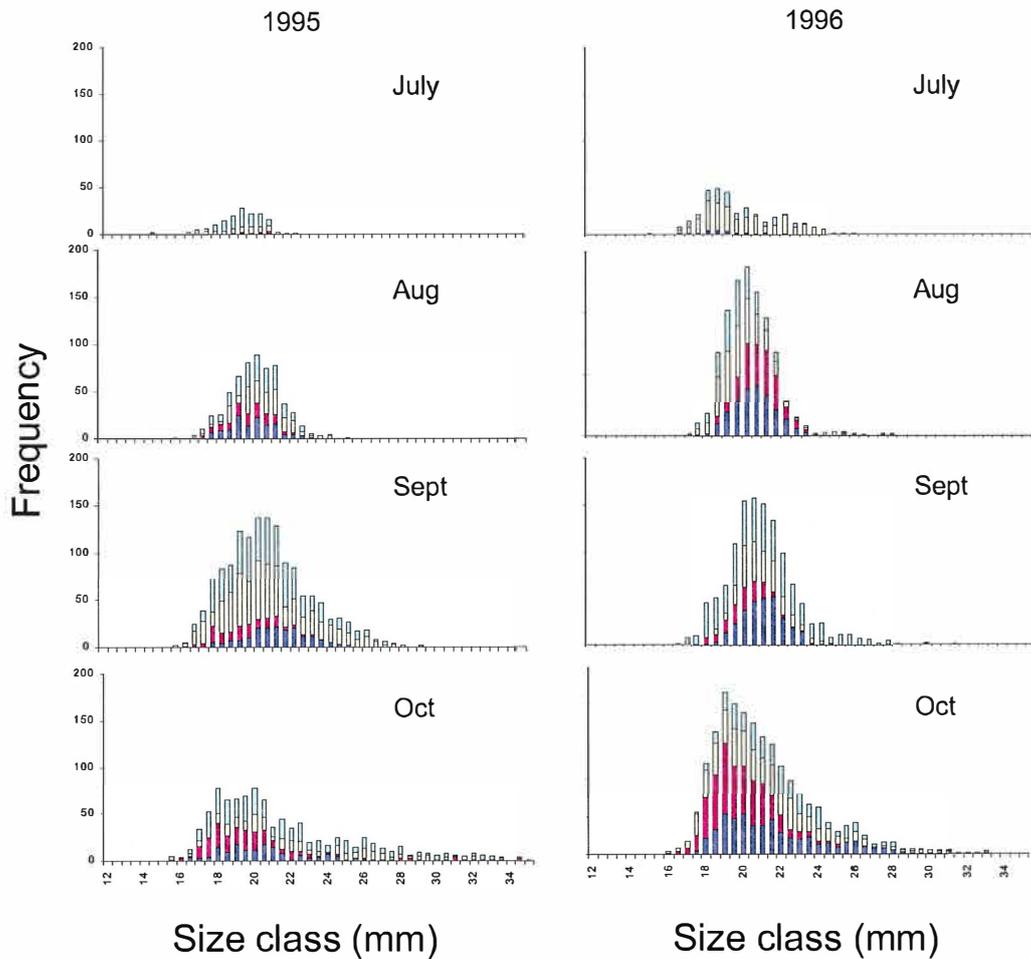
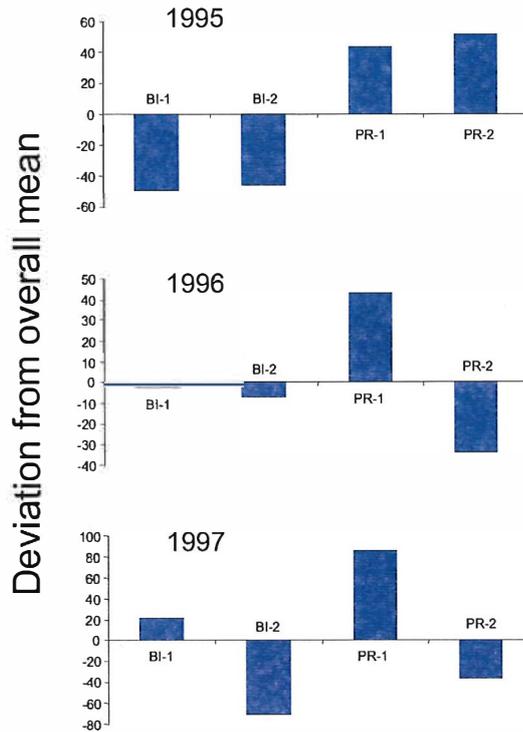


Fig. 5.4 Barker Inlet / Port River. Size frequency distributions of the samples collected on each sampling occasion, combined for the four sites (purple bars - BI-1, red bars - BI-2, yellow - PR-1, blue - PR-2).

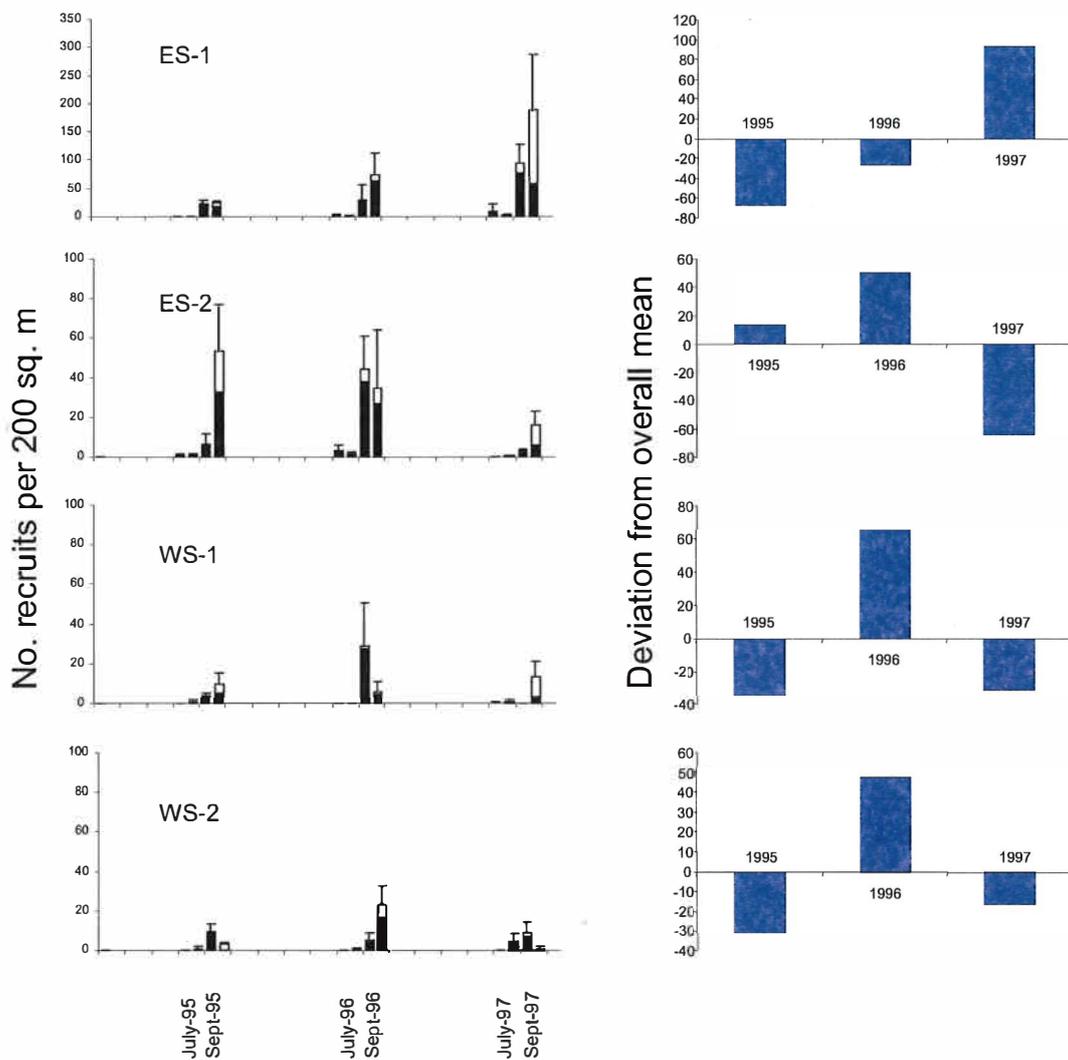


Fig. 5.5 Franklin Harbor. Left hand graphs show the catch rates from recruitment sampling on each sampling occasion at each site between 1995 and 1997. The numbers are divided by size - shaded bars for fish <20.5 mm SL, light bars for fish >20.5 SL. Right hand graphs show the deviation of the annual mean for each site from the overall mean for that site calculated across the three years.

Table 5.2 Results of the analysis of variance on the monthly recruitment counts recorded in the Franklin Harbor at the two sites within each place between 1995 and 1997. Prior to analysis the data were transformed using the $\ln(x + 1)$ transformation because of heterogeneous variances in the original data.

Factor	SS	Df	MS	F-ratio	probability
Year	3.5157	2	1.7579	0.7366	0.4893
Month	166.0379	3	55.3460	23.1903	0.0000**
Place	36.0566	1	36.0566	15.1079	0.0007**
Site	57.279	24	2.3866	7.3547	0.0000**
Year x Month	6.5833	6	1.0972	0.4597	0.8310
Year x Place	1.0333	2	0.5167	0.2165	0.8069
Month x Place	16.2633	3	5.4211	2.2715	0.106
Year x Month x Place	4.5883	6	0.7647	0.3204	0.9198
Residual	31.1528	96	0.3245		
Total	322.5102	143			

Fig. 5.6 Franklin Harbor. Graphs show the deviation of the annual mean for each site from the overall mean calculated across the four sites in each year.

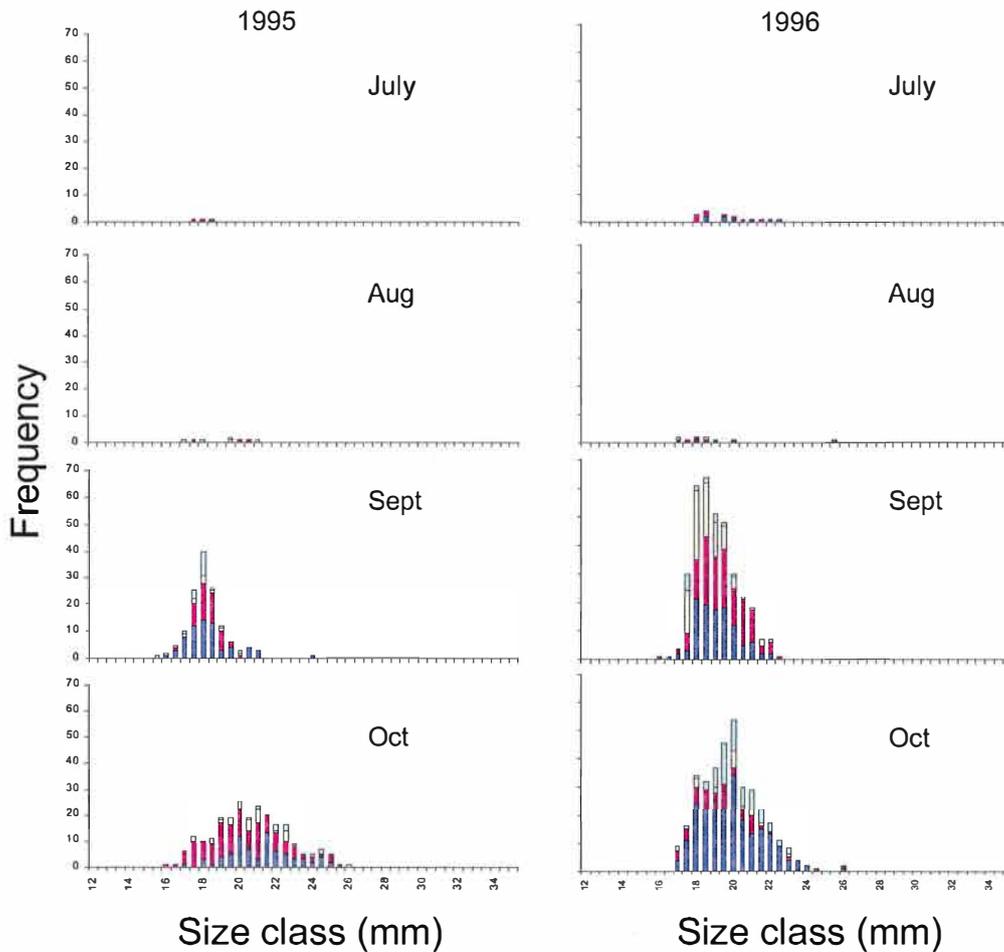
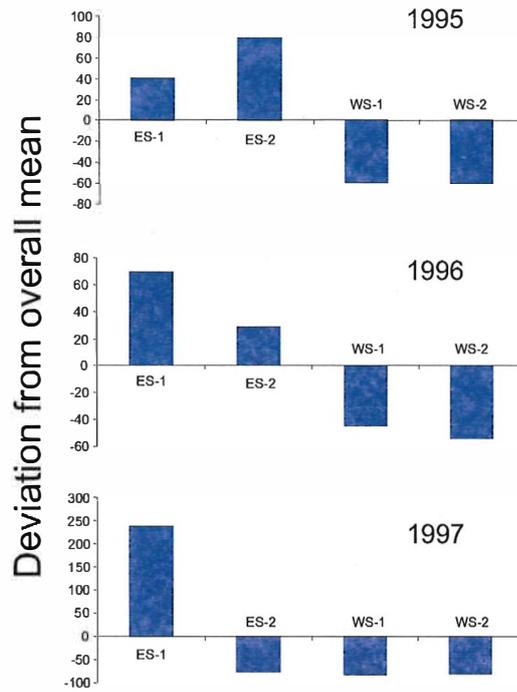


Fig. 5.7 Franklin Harbor. Size frequency distributions of the samples collected on each sampling occasion, combined for the four sites (purple bars -ES-1, red bars - ES-2, yellow - WS-1, blue - WS-2).

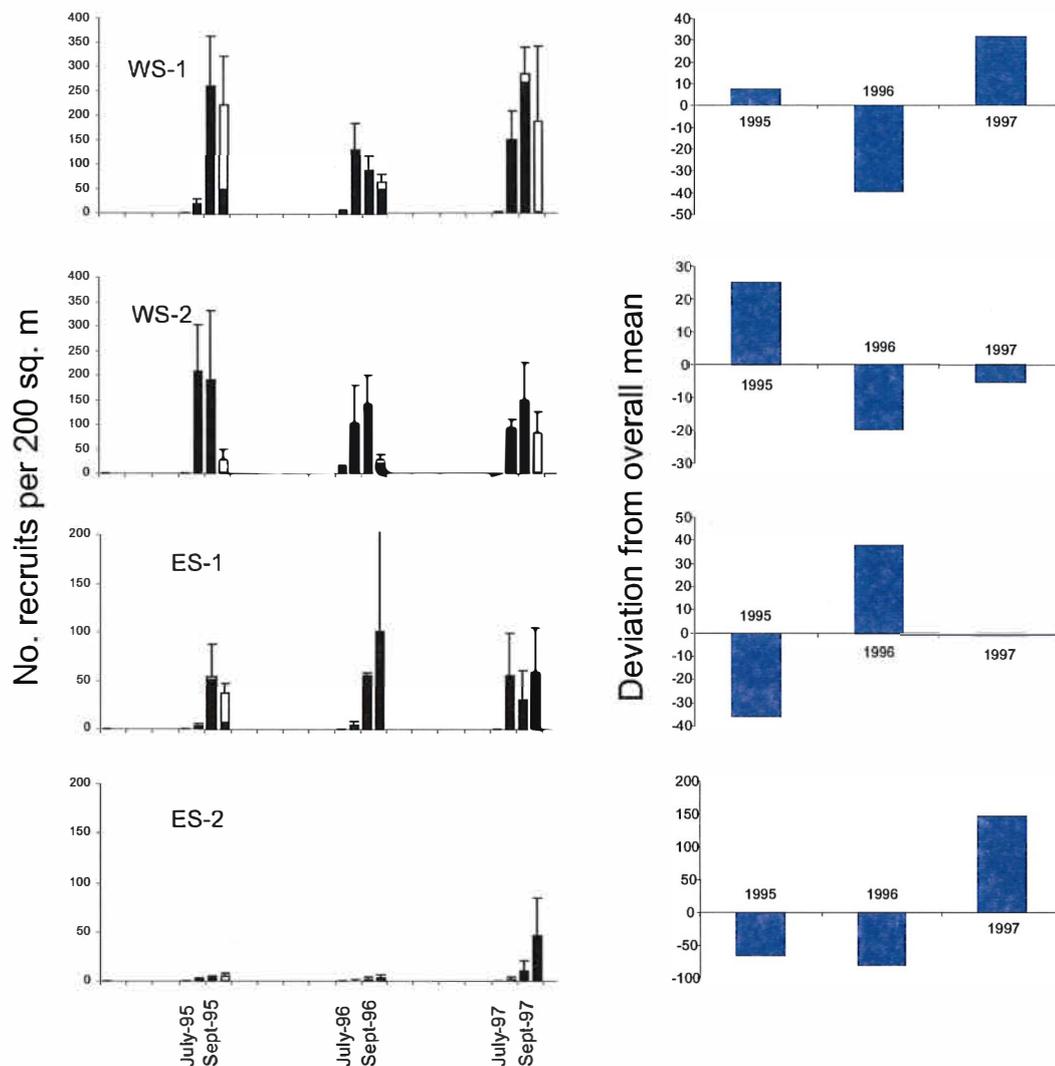


Fig. 5.8 Coffin Bay. Left hand graphs show the catch rates from recruitment sampling on each sampling occasion at each site between 1995 and 1997. The numbers are divided by size - shaded bars for fish <20.5 mm SL, light bars for fish >20.5 SL. Right hand graphs show the deviation of the annual mean for each site from the overall mean for that site calculated across the three years.

Table 5.3 Results of the analysis of variance on the monthly recruitment counts recorded in the Coffin Bay at the two sites within each place between 1995 and 1997. Prior to analysis the data were transformed using the $\ln(x + 1)$ transformation because of heterogeneous variances in the original data.

Factor	SS	Df	MS	F-ratio	probability
Year	5.1712	2	2.5856	0.7368	0.4892
Month	249.3925	3	83.1308	23.6901	0.0000**
Place	140.8182	1	140.8182	40.129	0.0105**
Site	84.2191	24	3.5091	6.6297	0.0000**
Year x Month	14.2269	6	2.3712	0.6757	0.6704
Year x Place	2.8079	2	1.404	0.4001	0.6746
Month x Place	34.5231	3	11.5077	3.2794	0.0383*
Year x Month x Place	72.2363	6	1.6294	0.4643	0.8277
Residual	50.8158	96	0.5293		
Total	591.7511	143			

Fig. 5.9 Coffin Bay.
 Graphs show the deviation of the annual mean for each site from the overall mean calculated across the four sites in each year.

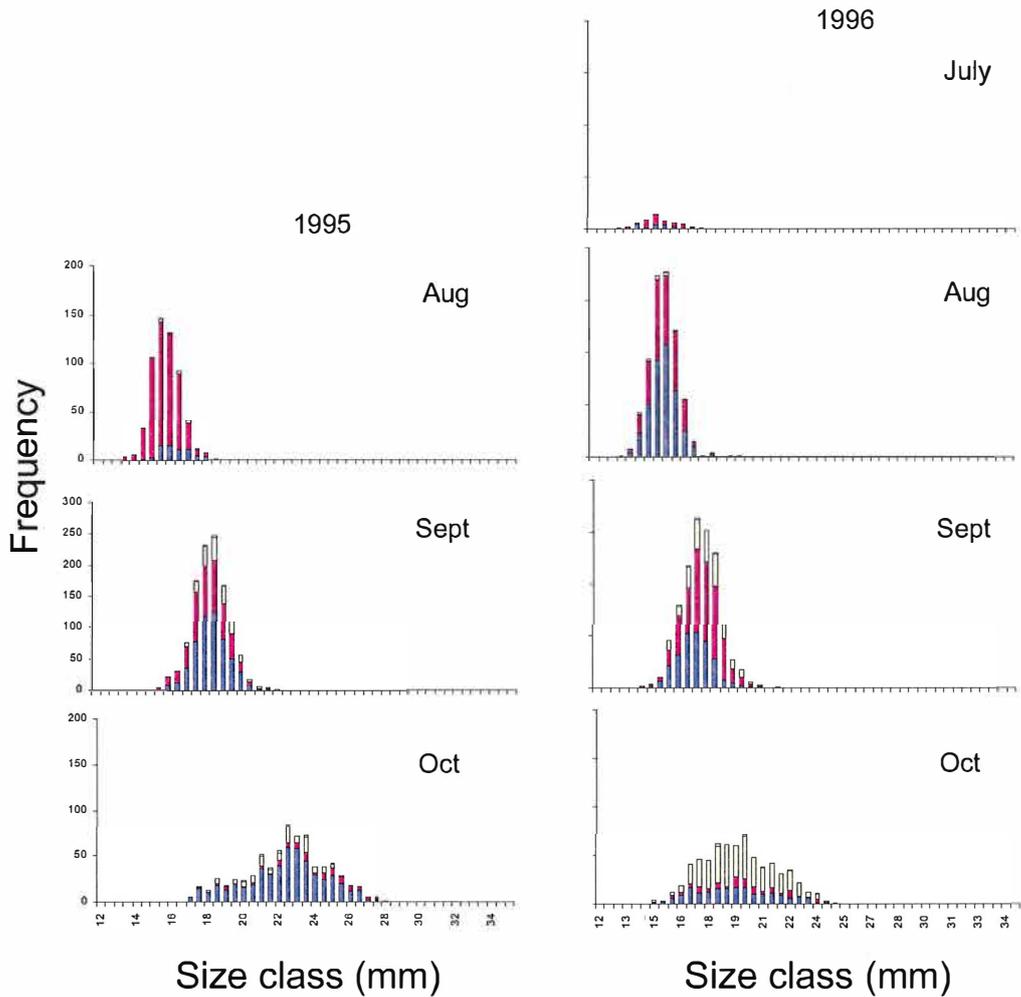
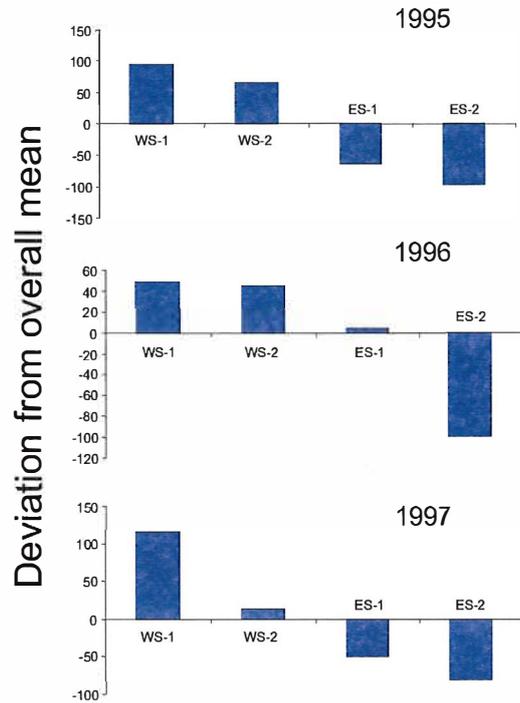


Fig. 5.10 Coffin Bay. Size frequency distributions of the samples collected on each sampling occasion, combined for the four sites (purple bars - WS-1, red bars - WS-2, yellow - ES-1, blue - ES-2).

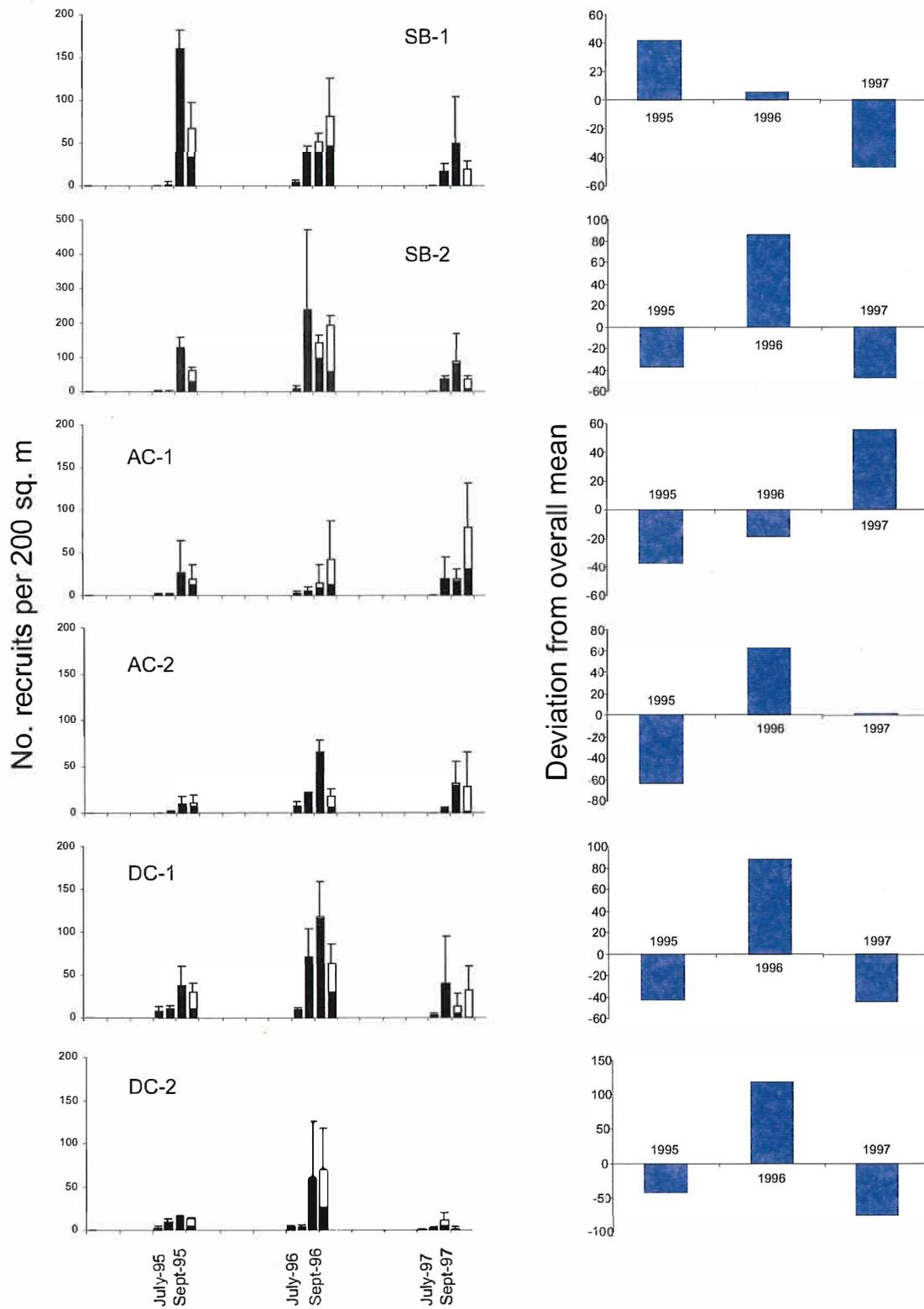


Fig. 5.11 Far West Coast. All conventions as in Fig. 5.2.

Fig. 5.12 Far West Coast. Graphs show the deviation of the annual mean for each site from the overall mean calculated across the four sites in each year.

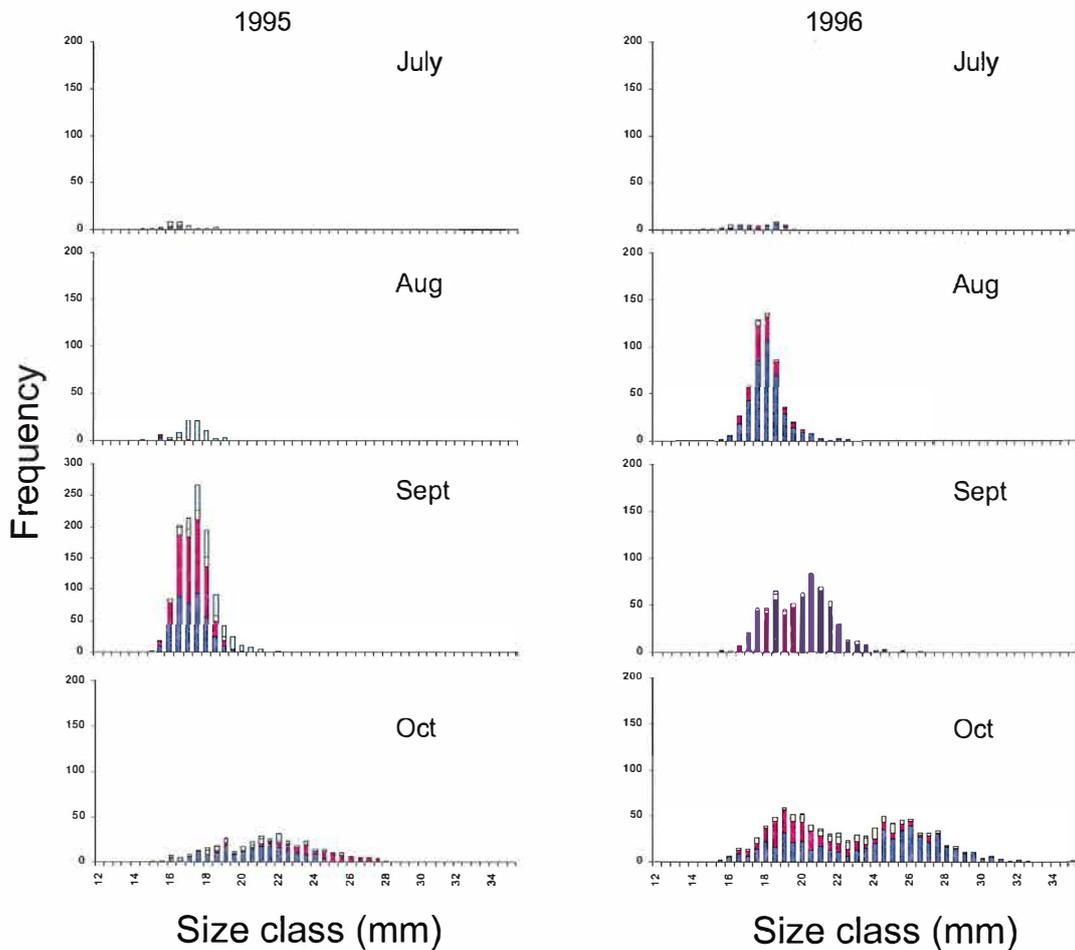
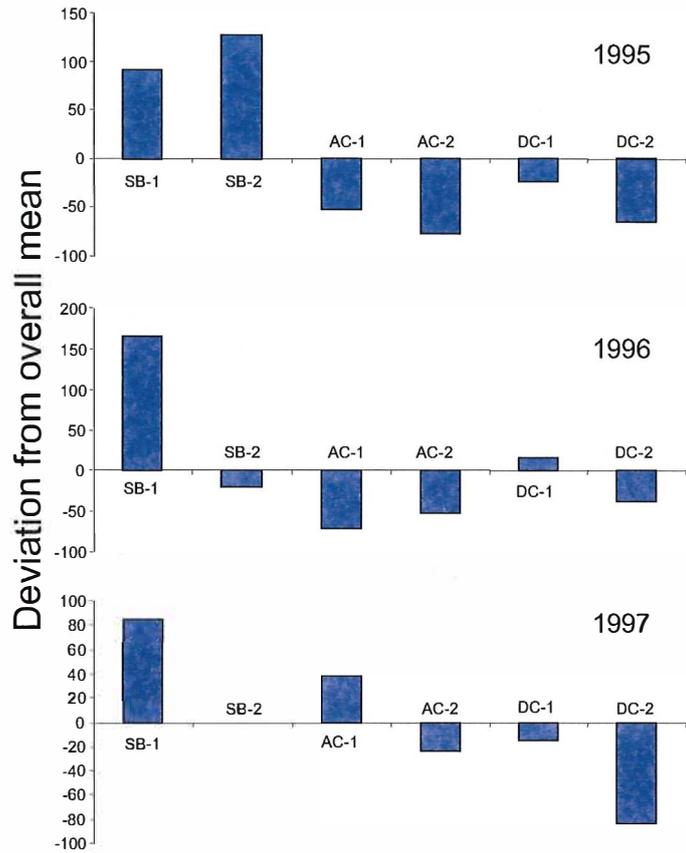


Fig. 5.13 Far West Coast. Size frequency distributions of the samples collected on each sampling occasion, combined for four sites (purple bars - SB-1, red bars - SB-2, yellow - AC-1, blue - AC-2).

Table 5.4 Results of the analysis of variance on the monthly recruitment counts recorded in the Streaky Bay, Acramen Creek and Davenport Creek at the two sites within each place between 1995 and 1997. Prior to analysis the data were transformed using the $\ln(x + 1)$ transformation because of heterogeneous variances in the original data.

Factor	SS	Df	MS	F-ratio	probability
Year	50.2746	2	25.1373	15.2467	0.0000**
Month	235.2075	3	78.4025	47.5541	0.0000**
Place	33.5534	2	16.7767	10.1757	0.0003**
Site	59.3527	36	1.6487	2.6674	0.0000**
Year x Month	24.1532	6	4.0255	2.4416	0.0440*
Year x Place	18.4107	4	4.6027	2.7917	0.0407*
Month x Place	23.449	6	3.9082	2.3705	0.0494*
Year x Month x Place	28.6323	12	2.386	1.4472	0.1904
Residual	89.0037	144	0.6181		
Total	562.0369	215			

Comparison of early life-history characteristics

For the analysis of estimates of age of the smallest post-larvae caught on the three occasions we excluded the October sample from Streaky Bay because of the lack of recent recruits. There was a general increase in mean age amongst sampling occasions, that was consistent across sites (Fig. 5.14). This substantial temporal effect accounted for 34.5% of the total variation in the data. Nevertheless, despite this, the mean ages of post-larvae from both sites on the west coast were generally younger than those from the two gulf sites, with those from Coffin Bay slightly younger than those from Streaky Bay (Fig. 5.14).

The sub-samples of small post-larvae selected for age analysis were measured prior to dissection for otolith removal. For each occasion the post-larvae from the west coast were significantly smaller than those from the gulfs, whilst those from Coffin Bay were significantly smaller than those from Streaky Bay (Fig. 5.14). This spatial difference was the dominant effect and accounted for 63.4% of the total variation in size, as compared to the 2.0% attributable to temporal variation.

The estimates of size and age were used to calculate average growth rate (Fig. 5.14). These also demonstrated substantial variation, with the dominant effect being the substantial decrease that occurred at each site between the first and the two subsequent sampling occasions. This temporal effect accounted for >50% of the total variation. Only on the third sampling occasion did the *a posteriori* tests identify a significant difference amongst growth rates at the different sites (Fig. 5.14).

Hatch dates also differed amongst sites and occasions (Fig. 5.15). The smallest post-larvae from the two west coast sites hatched on a significantly later date than those collected from the gulfs at approximately the same time (Fig. 5.15). In July the minimum difference between median dates was 17 days, whilst in September the median hatch dates were at least 13 days later than those from the two gulfs. In October the median hatch date for Coffin Bay was 12 days later than that from the gulfs.

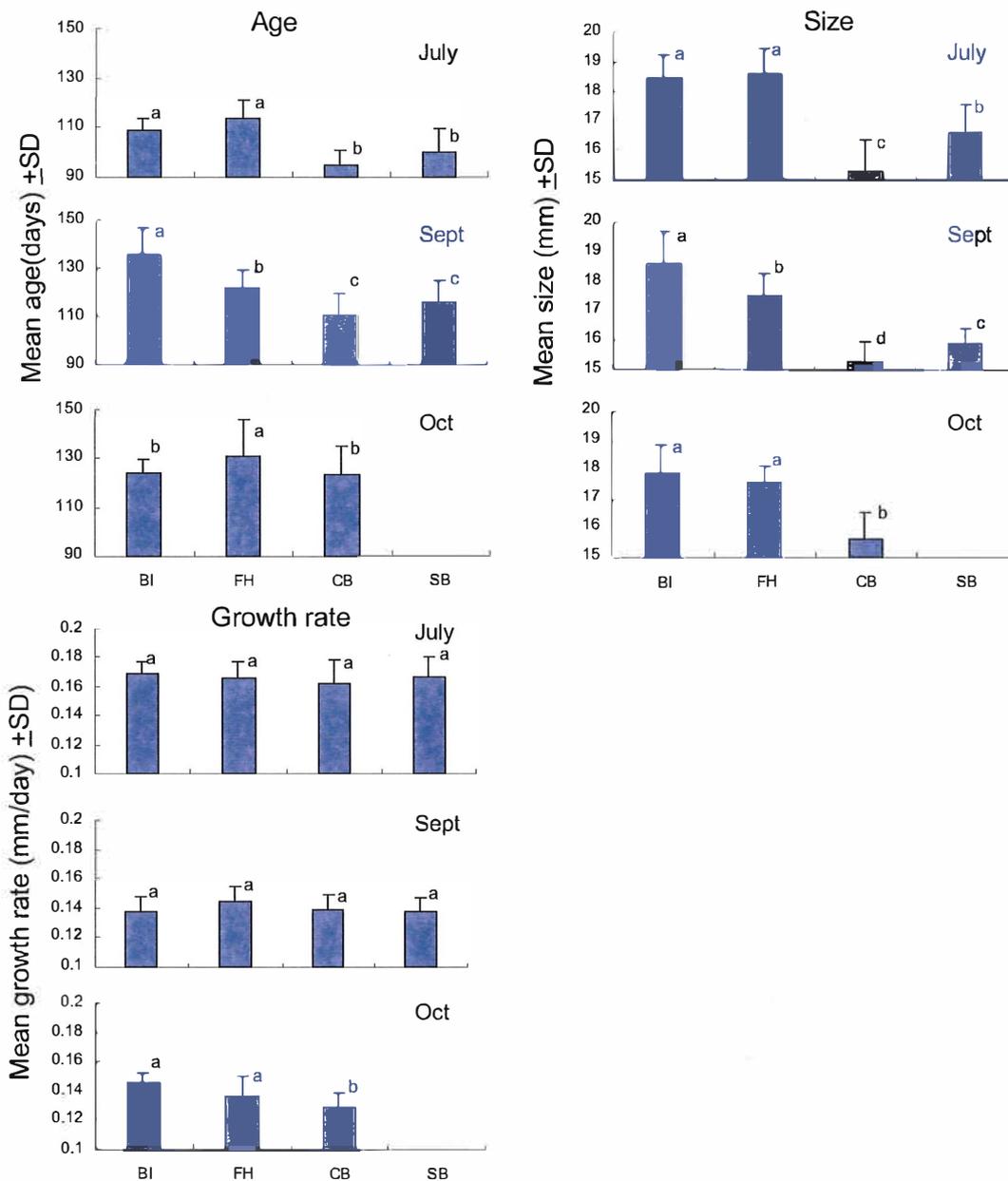


Fig. 5.14 Mean age, size and growth rates of the smallest post-larvae caught at each locality on each sampling occasion. Letters above histograms indicate the results of Student-Newman-Keuls tests comparing amongst localities for each occasion where means with same letter are not significantly different (BI, Barker Inlet; FH, Franklin Harbor; CB, Coffin Bay; SB, Streaky Bay).

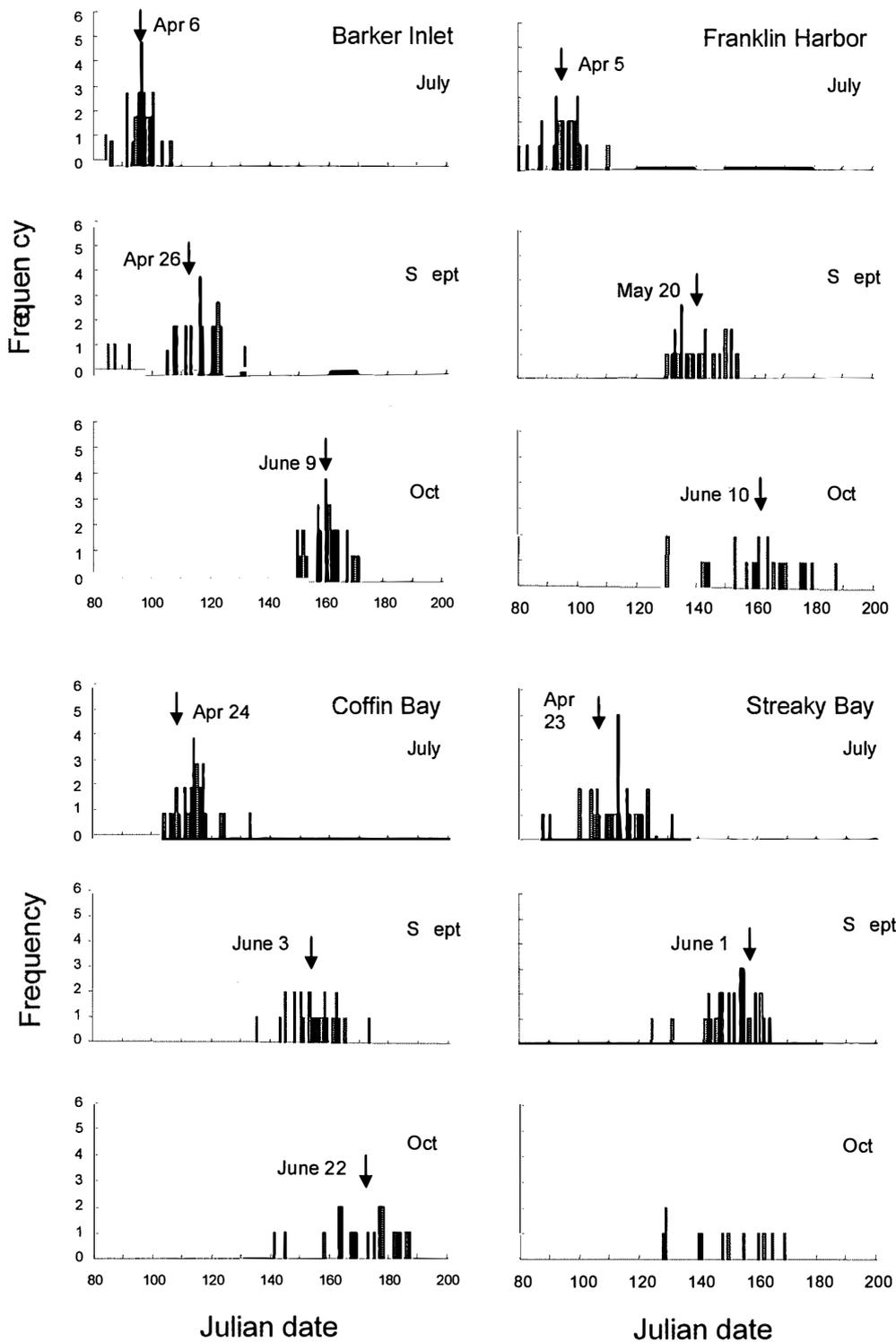


Fig. 5.15 Frequency histograms showing the number of post-larvae from each sample that hatched on the nominated Julian date. The median hatch date is shown for each sample site and date.

5.4 Discussion

Post-larval King George whiting recruit to shallow, sub-tidal beds of *Zostera* and *Heterozostera* spp. in South Australia, between July and November in each year (Fowler and Short 1996). It has previously been shown that such post-larvae are amenable to sampling using small seine nets in shallow, sub-tidal areas (Bruce and Short in prep.). In 1993 and 1994 we had used this technique and attained catches that ranged from zero up to 1,000 fish per 40 m transect (Fowler and Short 1996), and assumed that these numbers were indicative of the history of the rate of arrival of recruits and therefore provided a good recruitment index. In this study we applied the same sampling methodology in a hierarchical sampling program to examine the spatial and temporal variability in recruitment rates at several spatial scales. We sampled numerous sites separated by distances of metres to >500 kms. All sites were chosen for offering shallow, sub-tidal seagrass beds where it was possible to deploy the seine net. The limited availability of such sites constrained our sampling regime by, for example, limiting us to a single locality in each of Gulf St. Vincent and Spencer Gulf.

Recruitment rates

There was no consistent inter-annual variation in the recruitment rates amongst the four localities. For example, whilst the highest rates of input to the Barker Inlet/Port River were obtained in 1997, neither Franklin Harbor nor Coffin Bay displayed any substantial inter-annual variability (Table 5.5). Also, 1997 was a year of low recruitment at Streaky Bay and Davenport Creek. Such results suggest that recruitment did not vary in a systematic way across the entire area of the fishery, and suggested that recruitment rates were more likely the consequence of events occurring at least on a regional scale (i.e. Gulf St. Vincent, Spencer Gulf and the west coast). In fact even at the within-region spatial scale there was little conformity in the inter-annual variation in recruitment rates. For example, recruitment in 1997 was high at Acramen Creek, but low at Streaky Bay and Davenport Creek (Table 5.5).

At smaller spatial and temporal scales, however, there were some coherent recruitment patterns. Recruitment rates were generally lower in July and August than September and October. At Franklin Harbor and Coffin Bay the place closest to the entrance to the bay generally received higher input rates, presumably because of a depletion effect the further into the bay. Some sites also generally received higher recruitment, possibly reflecting the pattern of dispersion of post-larvae by local hydrodynamic phenomena. Hydrodynamic modelling has elucidated the small scale temporal and spatial aspects of recruitment of King George whiting in Port Phillip Bay (Jenkins et al. 1997, Jenkins et al. 1998). This study has determined that the delivery of post-larvae to particular sites around the bay was essentially passive and related to physical transport processes, i.e. tidal currents in some areas

and wind-driven currents in others. The numbers at each site also reflected the physical exposure of different locations particularly to wave action which influenced the mortality and movement of the early post-settlement recruits (Jenkins et al. 1997, Jenkins et al. 1998).

Table 5.5 Summary table showing the qualitative comparison of recruitment rates to the sample sites in each locality in the three years.

	BI/PR		Franklin Harbor		Coffin Bay		West coast		
	BI	PR	P1	P2	P1	P2	SB	AC	DC
1995	low	low	medium	low	high	low	medium	low	Low
1996	medium	low	medium	high	low	medium	medium	medium	high
1997	high	high	medium	low	medium	medium	low	high	Low

Not only did the recruitment rates to the 4 localities vary on an inter-annual scale there were substantial differences in the patterns of timing of recruitment between these. For example, Franklin Harbor did not receive significant recruitment until September, whilst significant recruitment had occurred in August at the other localities. The size structures also varied substantially between localities reflecting differences in the timing of recruitment but also differences in the characteristics of the early life-history. The most parsimonious explanation for such phenomena is that all recruits did not originate from a single spawning area, but originated from numerous different spawning grounds. The conclusion from the study of early life-history based on the analysis of otolith microstructure was similar.

Early life-history

Recruits to west coast bays experienced a shorter larval duration, settled at a younger age and therefore were spawned and hatched at significantly later dates than those caught at the same time in the two gulfs. They were also substantially smaller on arrival in the bays, a consequence of being younger. On first consideration such systematic spatial differences in size and age appear consistent with the post-larvae being delivered to the South Australian nursery areas from a westerly-located spawning region. Under such a scenario post-larvae would reach the west coast bays first because of their eastward transport and those reaching the gulfs would be older and larger by virtue of the greater distance travelled from the west. However, the data on early life-history characteristics from Streaky and Coffin Bays were not consistent with this hypothesis. Since there is a minimum of 200 km between Streaky and Coffin Bays the post-larvae would be expected to arrive at the latter bay

marginally older and larger than those that arrive at the former. In fact, however, the opposite to this occurred, i.e. the post-larvae from Coffin Bay were the smallest and youngest of the four sites. Consequently, such data are more consistent with the larvae originating from different spawning grounds and experiencing somewhat different environmental conditions through their larval phases.

A recent study used hydrodynamic modelling to determine the likely spawning grounds that provided the post-larvae which recruited to Barker Inlet, Franklin Harbor, Coffin Bay and Streaky Bay (Fowler et al. 2000). This study predicted that in each case it was likely that the spawning grounds were located only 40 - 150 km from each nursery area, and was abutted against the nearest coastline that was located either to the south or west of the nursery area. It suggested that such restricted larval movement was a consequence of the weak currents typical of the near-shore habitat of the main fishery area in South Australia. The results also suggested that major geographic features such as Eyre and Yorke Peninsulas may constitute significant barriers to larval transport, because of gyres that form in these areas. Frontal zones at the mouths of the gulfs may further restrict larval movement.

King George whiting in South Australia may consist of numerous, discrete, self-recruiting populations. We know through the analysis of tag/recapture information that adult King George whiting demonstrate only negligible movement in an east/west direction along the southern Australian coastline (Chpt 6). The current study has served to indicate that larval movement in this geographic region may also be highly restricted. The lack of conformity or systematic differences in the biological characteristics of recruitment to four distant nursery areas, suggested that recruitment was likely the consequence of local processes. However, the results from hydrodynamic modelling provided further evidence of limited larval movement and suggested that larvae are transported only over relatively short distances.

In contrast to the possible discrete stocks in South Australia, Victorian populations apparently conform to the concept of a single unit stock (Jenkins et al. 1997, Jenkins et al. 1998, Jenkins et al. 2000), because of the different physical oceanographic regimes between the two regions of southern Australia. The implications of these differences in population structure are substantial both for the spatial scale over which the population dynamics work and for fishery management. In South Australia population dynamics are likely determined on a small spatial scale, and may therefore be vulnerable to local over-fishing or recruitment over-fishing. Alternatively, in Victoria recruitment to nursery areas will be independent of local stock size, but will likely vary inter-annually with large-scale environmental influences on current regimes. These contrasting scenarios suggest that the spatial scale at which fishery management practises are applied must necessarily differ between the two regions.

5.5 References

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CHAPTER 6. ADULT MOVEMENT PATTERNS

A.J. Fowler and W.A. March

6.1 Introduction

The adults of many species of marine fish are capable of substantial movement, and incorporate such movement or migration as an obligate step in their life-history cycle (Wise 1963, Miller et al. 1984, Hilborn 1990). Such movement may represent seasonal or annual migrations, where fish spend part of the year in some places associated, for example, with feeding and then move to the spawning grounds for reproduction (Miller et al. 1984, Shimada and Kimura 1994). There are also movements associated with ontogenetic development where, as fish develop, they move to different places that present habitats that are more appropriate to the requirements of that life-history stage (Wise 1963, Hyndes et al. 1998). In both cases completion of the life-history and replenishment of the population through reproduction is dependent on fish movement.

Fishery managers and biologists need to understand the movement patterns of adult fish to:

1. understand the natural life-history of the species, the spatial scale over which it operates, and how fishers interact with this life-history at the smaller spatial scale;
2. to assess the interaction between fisheries in different locations;
3. to define the discreteness of stocks (Hilborn 1990).

For King George whiting in South Australia the uneven size and age distributions of the populations suggest the possible significance of adult movement (Chpt 3). Furthermore, in Western Australia post-larvae and juveniles occur in estuaries, whilst adults are associated with off-shore limestone reefs at 6 – 50 m in depth, thus implicating off-shore movement and its association with ontogenetic development (Hyndes et al. 1998). The confamilials *Sillago bassensis*, *S. vittata* and *S. burrus* also display size-related shifts from shallow, near-shore to deep, inner-shelf waters (Hyndes et al. 1996).

The most tractable method for directly monitoring the movement of adult fish is through tag/recapture programs. For King George whiting in South Australia there is a considerable history of tagging studies that date back to the 1930's. Since the 1960's approximately 26,000 fish have been tagged throughout a large part of the state, from which there have been >2,500 recaptures (Table 6.1). The analyses of these data are presented in this chapter, addressing the specific questions of:

1. which fish move ?;
2. from where and to where do they move ?;
3. what size are they when they move ?

Table 6.1 Summary of the history of tag/recapture programs for King George whiting in South Australia.

Year	Location	Number tagged	Number recaptured
1937-40	Venus Bay, Coffin Bay Kangaroo Island	?	26
1963-64	Kangaroo Island	100	0
1963-69	Ceduna	1,496	308
1966-67	Venus Bay, Baird Bay	1,700	336
1968	Gulf St. Vincent	82	4
1968	Franklin Harbor	716	150
1969	Northern Spencer Gulf	?	133
1978-82	Gulf St. Vincent	2,620	145
1979-85	Ceduna	1,448	68
1977-80	Coffin Bay	2,426	330
1977-85	Northern Spencer Gulf	1,807	73
1978-85	Southern Spencer Gulf	3,263	129
1977-85	Kangaroo Island	2,909	137
1986-87	Gulf St. Vincent	7,341	741
Total		>25,908	2,580

6.2 Methods

Tag/recapture data collected between the 1960s and 1980s were analysed in this study. Data on tag returns from fish tagging through 1963-1969 were entered to computer from original datasheets, whilst that from the 1970-80s had previously been entered to Lotus worksheets. All tag/recapture sites were allocated a latitude and longitude. The data were downloaded to ACCESS databases, and records were extracted for fish that had been at large for >30 days, and for which both a tag and recapture location were recorded. These were read into the GIS program MAPINFO, which was used to estimate the minimum net distance between the place of tagging and that of recapture. The lines showing the minimum net distances between tag and recapture sites for all recaptured fish were drawn onto maps.

6.3 Results

Eastern Region

Gulf St. Vincent

Our most comprehensive dataset on fish movement was for fish tagged in Gulf St. Vincent in 1986-87 (Table 6.1). Of the 741 recaptures, 492 were at liberty for >30 days, and both the tag and recapture locations were known. At the time of tagging these fish ranged from 200 – 420 mm TL, and had a modal size of 300 mm (Fig. 6.1a). The size distribution at recapture was skewed to the right, although the mode remained at 300 mm. 84.7% of recaptures were estimated to be 3 years old or less, whilst 99.4% were 5 years or less.

For most fish the distances between tag and recapture sites were <20 km (Fig. 6.1b). The remaining fish moved net distances of up to 170 km, except one individual that moved 420 km around to Coffin Bay (not shown on Fig. 6). There was little relationship between distance moved and size at tagging, indicating that fish tagged at the larger sizes (i.e. >350 mm TL) moved similar distances to those tagged when small (Fig. 6.1c). There was an interactive influence of fish size and time-at-liberty on distance moved. Fish in the 200-249 mm class were not caught more than 30 km from the tag site, until several hundred days after initial capture (Fig. 6.1c), by which time they would have grown much larger. This suggests that small fish did not move long distances. Several in the 250-299 mm class moved 20-60 km within a month or two of tagging, whilst some in the next largest size group were recaptured >160 km from the tag site after only a few weeks of being tagged. The average rate of movement was size-related. Whilst most fish showed only a slow rate of movement, numerous fish that were >300 mm TL did move in excess of an average of 0.5 km day⁻¹ (Fig. 6.1d).

A total of 188 fish were tagged and recaptured within the same autumn/winter period, many of which were tagged in the vicinity of the Barker Inlet system (Fig. 6.2a). There were numerous recaptures in this vicinity. Some that made substantial movements were headed southwards along the metropolitan coastline, whilst others moved to the north-west along the coast, some ending up at the head of the gulf. In contrast, in spring/summer most substantial movements were directed southwards (Fig. 6.2b). For fish at liberty for 6-12 months, the smallest ones made some southward progress along the metropolitan coastline. However, most obvious were the southward-directed movements of fish that were >260 mm at the time of tagging. For fish at large for 12-24 months, those from Barker Inlet were recaptured along the south-eastern shore of the gulf, had crossed the gulf to the south-western shore or were recaptured on the northern coast of Kangaroo Island or the southern coast of Yorke Peninsula (Fig. 6.2d). Of the 10 fish from Gulf St. Vincent that were at liberty for >24 months, 7 left the gulf

and were recaptured along the northern coast of Kangaroo Island (Fig. 6.2e). Two of the remaining 3 fish were recaptured not far from the original tag site.

Kangaroo Island

Of the 2,909 fish tagged in Blocks 41 & 42 around Kangaroo Island, 137 were recaptured, of which 109 provided usable data. At tagging these 109 fish ranged from 220 to 460 mm and were unimodally distributed around 320 mm TL (Fig. 6.3a). The size distribution at recapture was also unimodal and distributed around the mode of 360 mm. At recapture, 90% of the fish were estimated to be ≤ 4 years old, and 97.2% ≤ 5 years.

Despite that many fish were at large for >1 year, only 3 moved >30 km (Fig. 6.3b). Of those that moved less, there was little relationship between distance moved and size at initial capture. Fish tagged at sizes of >350 mm TL were recaptured at similar distances from tag sites as those tagged at smaller sizes. Those >250 mm TL moved distances of up to 20 km within a few months of initial capture. The three fish that moved the greatest distances were recaptured >1 year after tagging (Fig. 6.3c). The smallest fish demonstrated the lowest rate of movement, but for fish >250 mm TL there was no relationship between movement rate and size (Fig. 6.3d).

All recaptured fish were initially tagged in the shallow north-eastern bays of the island (Fig. 6.2f). The results presented on the map demonstrate that most movement was restricted to within this relatively small area. Of the three fish that moved furthest, 2 moved to the north-western coast of the island, and the last crossed Backstairs Passage to near Cape Jervis.

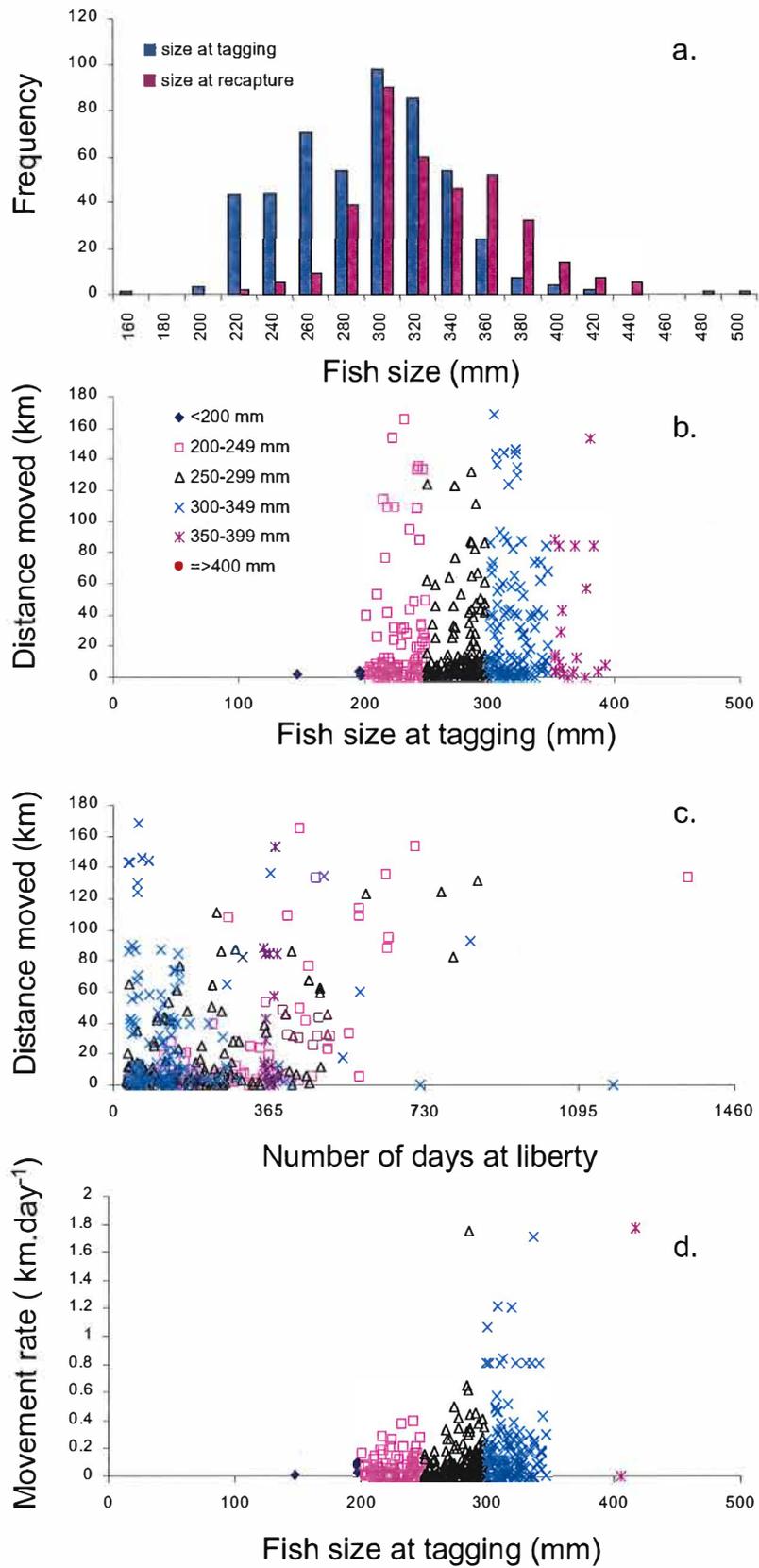


Fig. 6.1. Characteristics of fish movement from fish tagged in Gulf St. Vincent. a. Frequency distributions of tag and recapture sizes. b. Relationship between distance moved and size at tagging. c. Relationship between distance moved and time at liberty. d. Relationship between rate of movement and size at tagging.

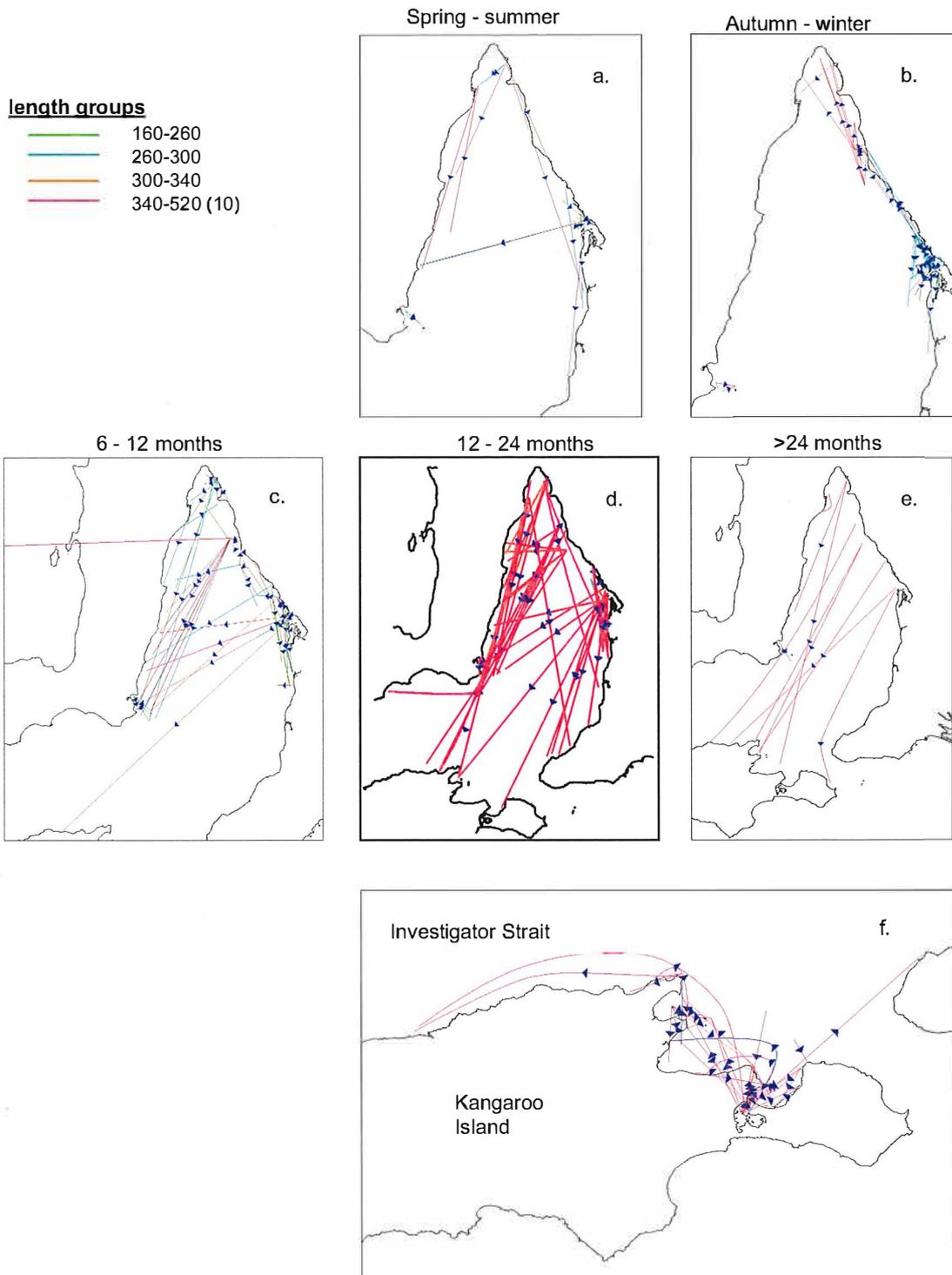


Fig. 6.2 Maps showing the paths of minimum net distance between places where individual fish were initially tagged and then recaptured; arrowheads indicate the direction of movement. Maps a to e relate to fish tagged in Gulf St. Vincent and recaptured during the indicated seasons, or after the nominated period. Map f relates to fish tagged in the north-east bays of Kangaroo Island. For maps a, b, c line colour indicates the release length group, for maps d, e, f it indicates return length.

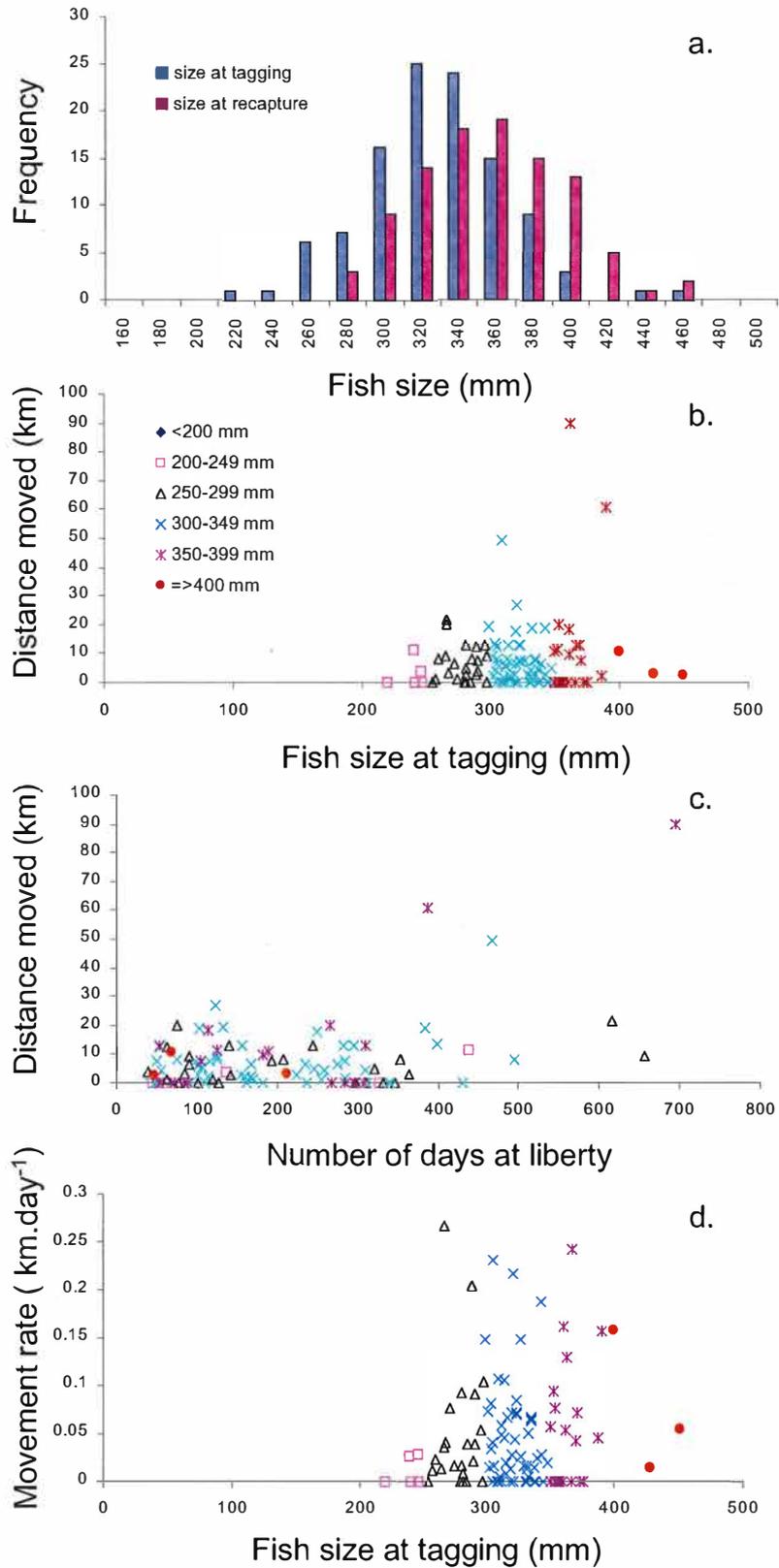


Fig. 6.3 Characteristics of fish movement from fish tagged at Kangaroo Island. a. Frequency distributions of tag and recapture sizes. b. Relationship between distance moved and size at tagging. c. Relationship between distance moved and time at liberty. d. Relationship between rate of movement and size at tagging.

Spencer Gulf

Northern Spencer Gulf

Useful information was available for 236 fish tagged in northern Spencer Gulf during the 1960s and 1970s. The sizes at tagging were bimodally distributed with modes at 240 and 320 mm TL (Fig. 6.4a). Size range at recapture was 280-480 mm, of which 81.2% were estimated to be ≤ 3 years, with the remainder ≤ 5 years.

The range of net movements was 0 – 305 km, although few exceeded 250 km (Fig. 6.4b). There was little relationship between distance moved and release length, indicating that regardless of whether fish were first captured at < 200 mm or were approaching 400 mm, some of that size group moved up to 250 km before capture. Fish tagged at a size of < 250 mm TL were recaptured less than 50 km from the tag site in the first year, but up to 250 km away approximately 1.5 years after tagging (Fig. 6.4c). Most in the 200-249 mm class moved < 100 km within the first year of capture, and some had moved > 200 km after 2 years. Some fish between 250-399 mm TL moved up to 200 km within only a few months of capture. For these size classes there was little relationship between distance moved and time at liberty. There was no apparent relationship between rate of movement and size at tagging (Fig. 6.4d).

Patterns of movement are evident in Fig. 6.5. During the 1960s many fish were tagged in the very north of Spencer Gulf and in Franklin Harbor. Of the former, many were recaptured in the south-eastern part of the gulf, particularly in Hardwicke Bay (Fig. 6.5a). Some were recaptured in the central part, and others along the north-western coast. In general, fish initially tagged in Franklin Harbor followed the south-west coast and ended up around the islands of the south-western part of the gulf. There were few instances of fish crossing from one side of the gulf to the other. Two fish, one originating in the north and the other from Franklin Harbor left the gulf and were later recaptured in Coffin Bay.

Of the 54 fish for which data were collected in the 1970s-80s most were tagged in Franklin Harbor or in the north-east (Fig. 6.5b). Although a few moved northwards or crossed the gulf most were recaptured along the south-western coastline. None of these fish left the gulf.

Southern Spencer Gulf

A total of 99 recaptures provided information on movement patterns in southern Spencer Gulf. These were initially bimodally distributed with the modes at 260 and 380-400 mm TL (Fig. 6.6a). Sizes at

recapture were skewed towards the larger fish, with one mode at 400 mm TL. The ages of 92% of the recaptured fish were estimated at 1 - 5 years, and most were between 2 – 4 years.

Distances moved were generally quite small. Only 5 fish moved >40 km, one of which exceeded 100 km (Fig. 6.6b). A total of 76.8% of fish were recaptured within 10 km of the tag site. For the remainder there was little relationship between size at tagging and distance moved, apart from the fact that the 5 fish that moved >40 km all exceeded 300 mm TL at tagging (Fig. 6.6b).

There was an interactive influence between fish size and time at large, that affected the distance moved. Fish <250 mm TL were captured >20 km from the tag site, only after periods of >1.5 years after tagging (Fig. 6.6c). Those <300 mm TL were caught at >20 km distance at least 6 months after tagging. Alternatively, a few fish tagged when >350 mm TL moved between 60 – 80 km within a few months of initial capture. All fish <300mm TL showed a very slow rate of movement whilst some larger ones demonstrated a faster movement rate (Fig. 6.6d).

The map shows the 25 fish that moved the largest distances (Fig. 6.5c). Those tagged in the inshore areas of Hardwicke Bay moved short distances off-shore. Some of those tagged in the central or western parts of the gulf moved considerable distances to the north-west. No fish tagged in southern Spencer Gulf was recaptured outside the gulf.

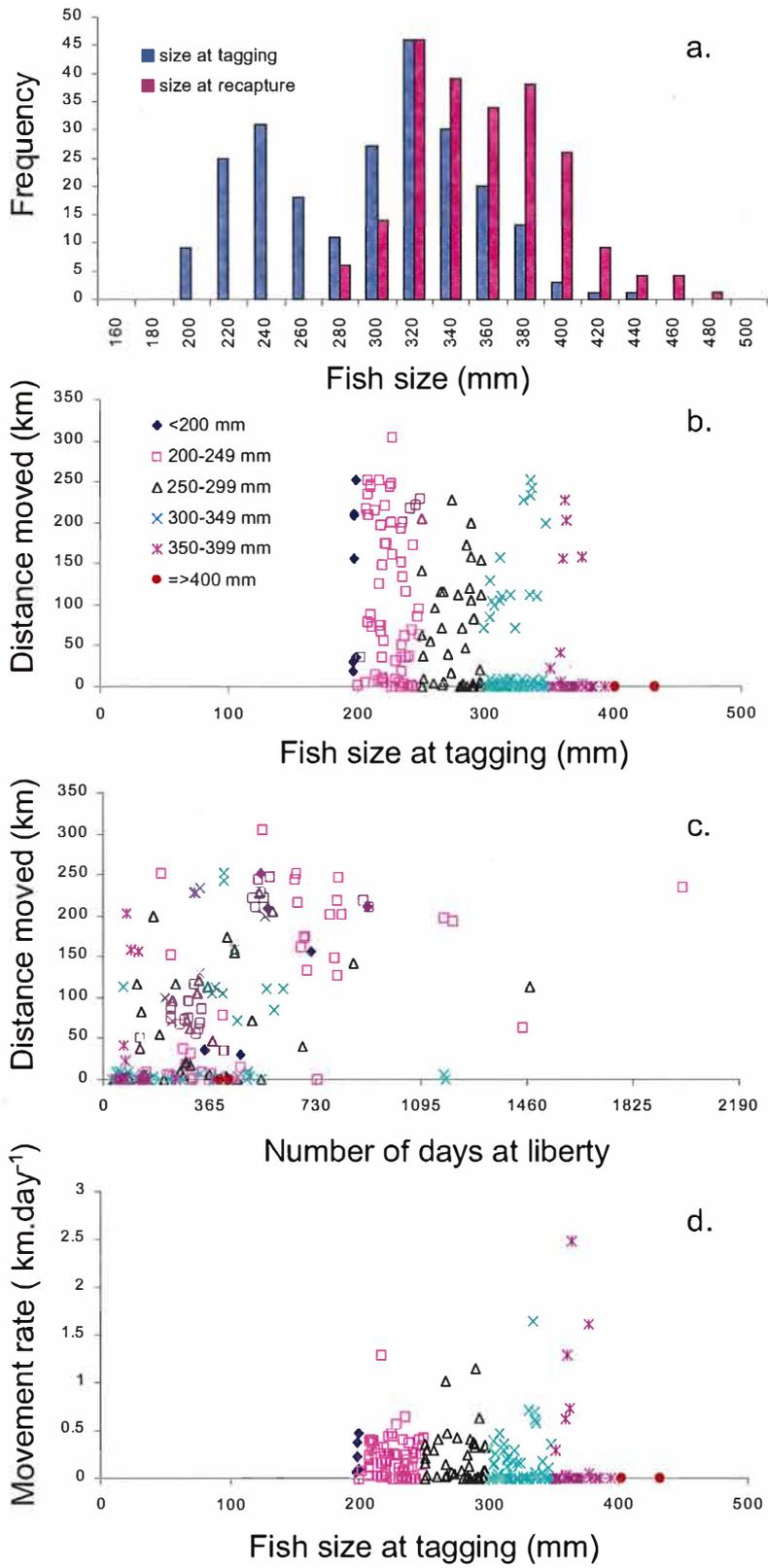


Fig. 6.4 Characteristics of fish movement from fish tagged in northern Spencer Gulf. a. Frequency distributions of tag and recapture sizes. b. Relationship between distance moved and size at tagging. c. Relationship between distance moved and time at liberty. d. Relationship between rate of movement and size at tagging.

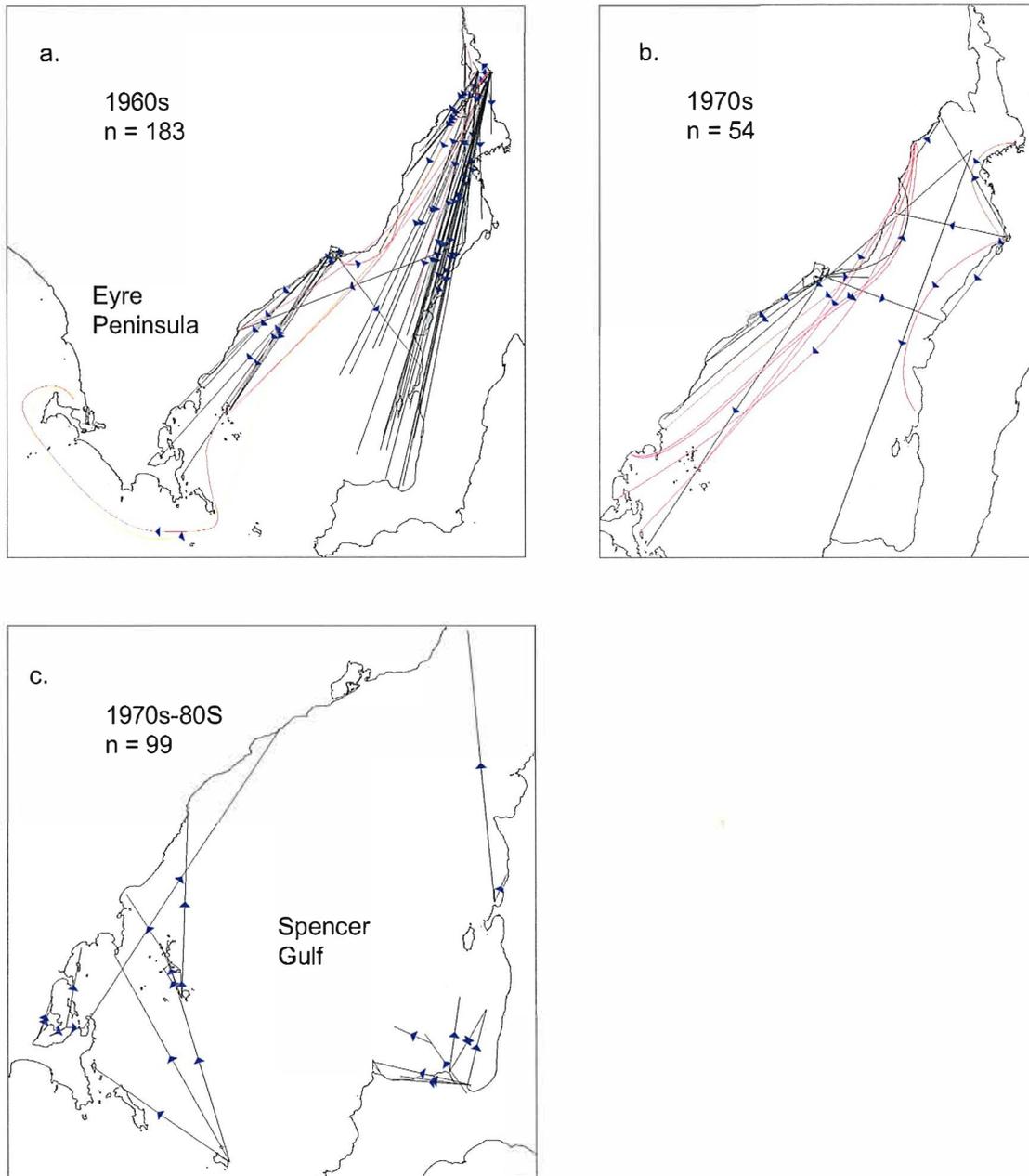


Fig. 6.5 Maps showing the paths of minimum net distance between places where individual fish were initially tagged and then recaptured; arrowheads indicate the direction of movement. Maps a and b relate to fish tagged and recaptured in Northern Spencer Gulf in the 1960s and 1970s. Map c relates to fish tagged in southern Spencer Gulf.

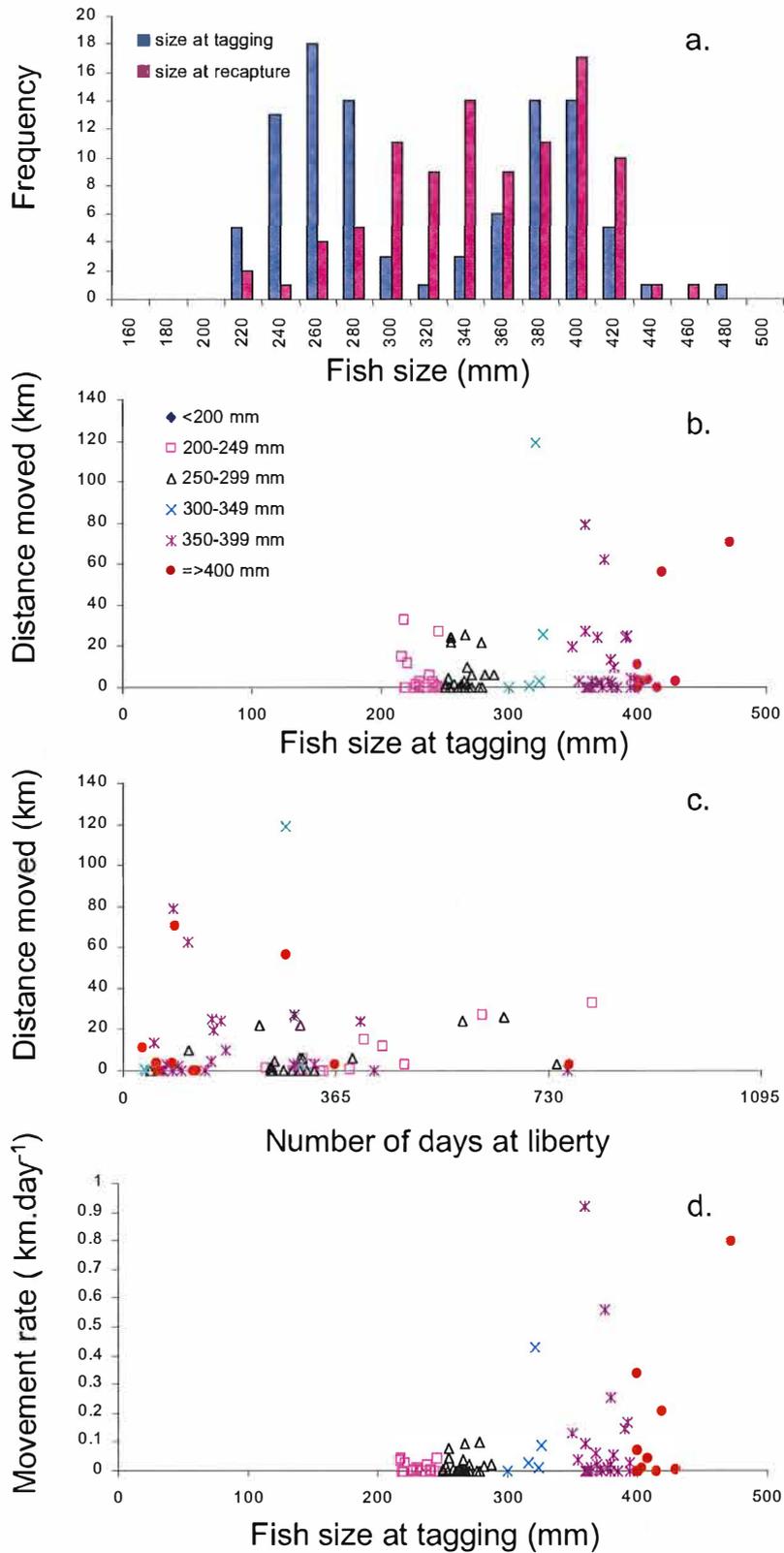


Fig. 6.6 Characteristics of fish movement from fish tagged in southern Spencer Gulf. a. Frequency distributions of tag and recapture sizes. b. Relationship between distance moved and size at tagging. c. Relationship between distance moved and time at liberty. d. Relationship between rate of movement and size at tagging.

West Coast

Coffin Bay

A total of 248 fish provided useful tag/recapture data. These covered the size range of 240-420 mm TL, and were bimodally distributed with modes at 260 and 340 mm TL (Fig. 6.7a). Sizes of recaptures were unimodally distributed around 320 mm TL, and 96% of these were estimated to be ≤ 3 years of age.

All but 9 fish were recaptured less than 50 km from the tag location (Fig. 6.7b). Of those that exceeded this distance, 8 were less than 300 mm TL at tagging. They were recaptured, however, at least several months after tagging (Fig. 6.7c). Relatively few fish exceeded a rate of movement of $0.4 \text{ km}\cdot\text{day}^{-1}$, and the rate of movement was largely independent of size (Fig. 6.7d).

Most fish were tagged either within Coffin Bay, at Point Longnose or at Point Sir Isaac. Of the 248 recaptures, all but 11 were recaptured within this general area (Fig. 6.8a). Two had moved around into Spencer Gulf, and 8 moved along the north-west coast, and were recaptured at Drummond Point, and at Anxious, Streaky, Sceale and Denial Bays.

Venus and Baird Bays

Of the 1,700 fish tagged in Venus and Baird Bays during the 1960s, there were 336 recaptures, of which 219 provided useful data (Fig. 6.9a). Size at tagging was unimodally distributed with the mode at 300 mm TL. At recapture, most fish were still small, although a few had reached 400 mm TL. All fish were estimated at < 3.5 years of age at recapture.

All but 3 fish were recaptured within 20 km of the tag site (Fig. 6.9b). The three exceptions were in the 250-299 mm TL size class when tagged, but were recaptured at least 200 days after tagging (Fig. 6.9c). The smallest fish (i.e. < 250 mm TL) moved at the slowest rate. However, for those larger than this size the rate of movement was largely independent of tag size.

Movement was generally restricted to within the bay where fish were originally tagged (Fig. 6.8b). Of the four that left either bay, one was caught just outside, one moved from Baird to Venus, one in the opposite direction, and one moved from Venus Bay up the coast to near Smoky Bay.

Denial Bay

Of the 2,944 fish tagged in Denial Bay between the 1960s-80s, 376 were recaptured and 158 provided useful data (Fig. 6.10a). Sizes of fish at tagging were from 200-400 mm TL, with the mode around 300 mm. Fish were on average much larger at recapture, with the modal size at 360 mm TL. A total of 96% of recaptures were estimated to be <3.5 years old.

All fish were recaptured within 40 km of the tag site (Fig. 6.10b). There was no relationship between distance moved and size at tagging, indicating that larger fish (i.e. >350mm TL) moved the same distances as smaller ones. Some fish in the 250-350 mm size range moved up to 15 km within a short period of tagging (Fig. 6.10c). There was no tendency for distance moved to vary with time at large. Rate of movement was independent of size (Fig. 6.10d).

The maps reveal some movement into and out from Denial Bay (Fig. 6.8). Some recaptures were made along the coast to the west. Also, some fish were caught off-shore in the vicinity of St. Peter and Eyre Islands.

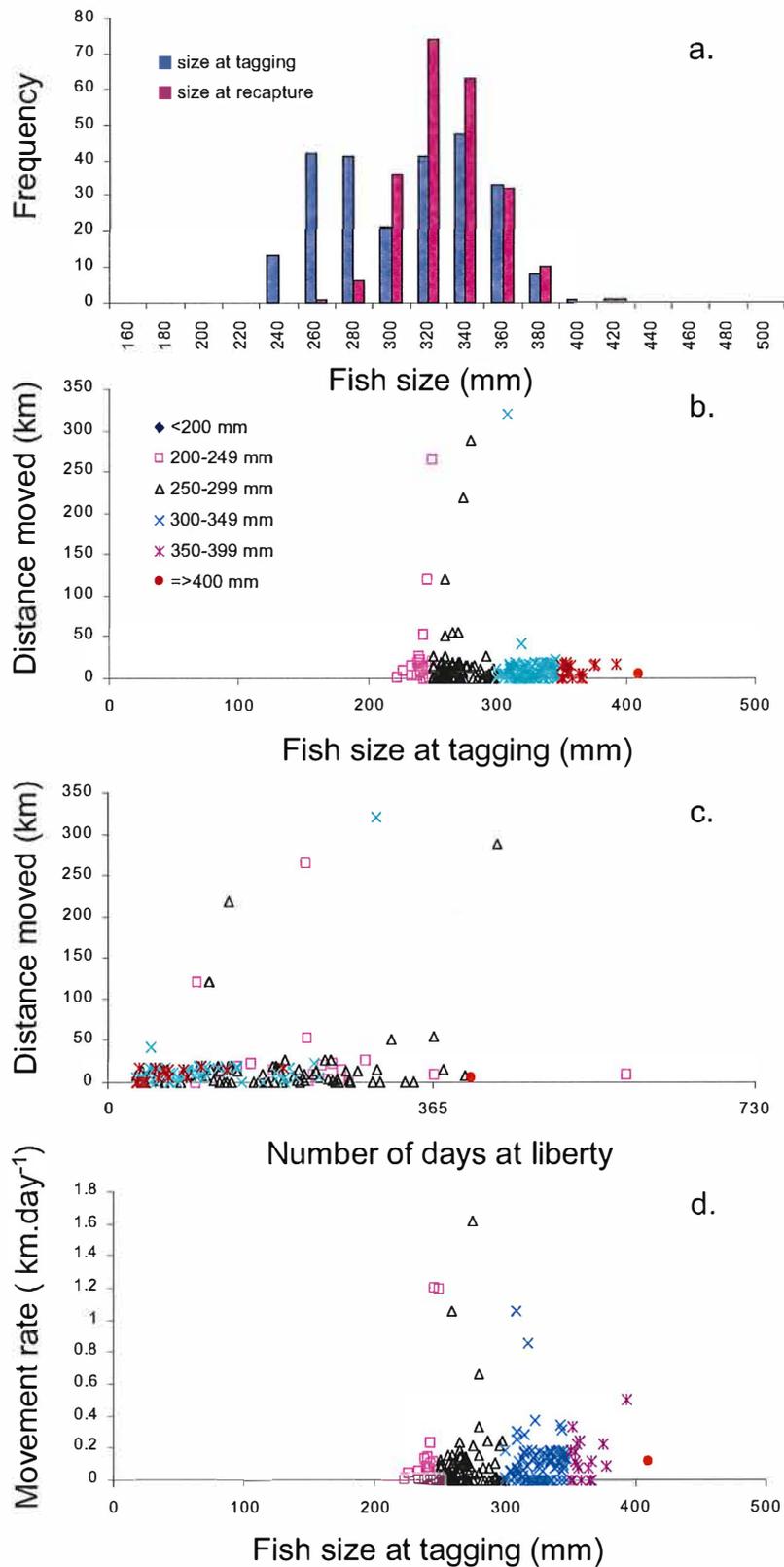


Fig. 6.7 Characteristics of fish movement from fish tagged in Coffin Bay. a. Frequency distributions of tag and recapture sizes. b. Relationship between distance moved and size at tagging. c. Relationship between distance moved and time at liberty. d. Relationship between rate of movement and size at tagging.

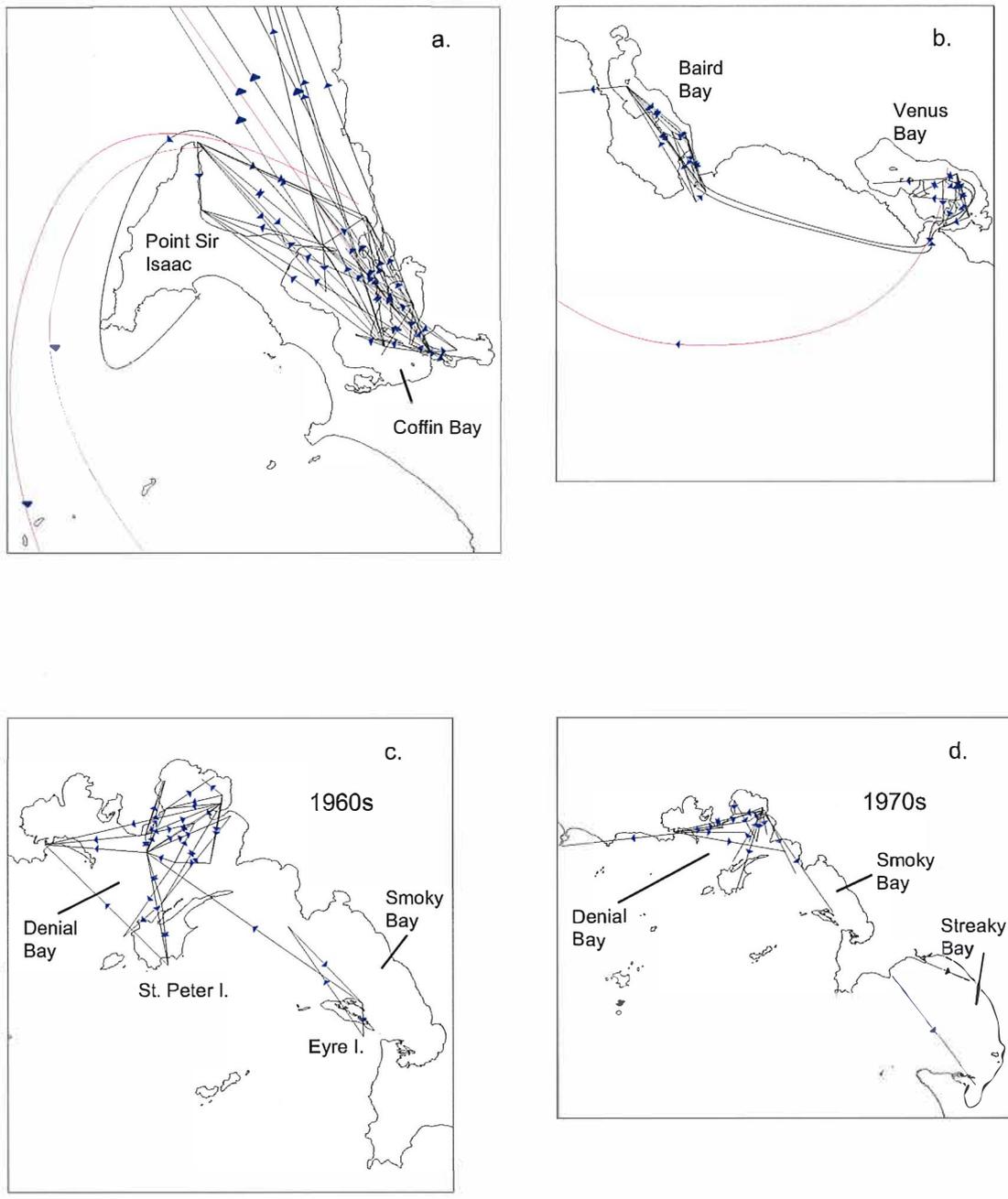


Fig. 6.8 Maps showing the paths of minimum net distance between places where individual fish were initially tagged and then recaptured; arrowheads indicate the direction of movement. Map a relates to fish tagged in Coffin Bay; Map b to those in Baird and Venus Bay; and Maps c and d to those in Denial Bay in the 1960s and 1970s, respectively.

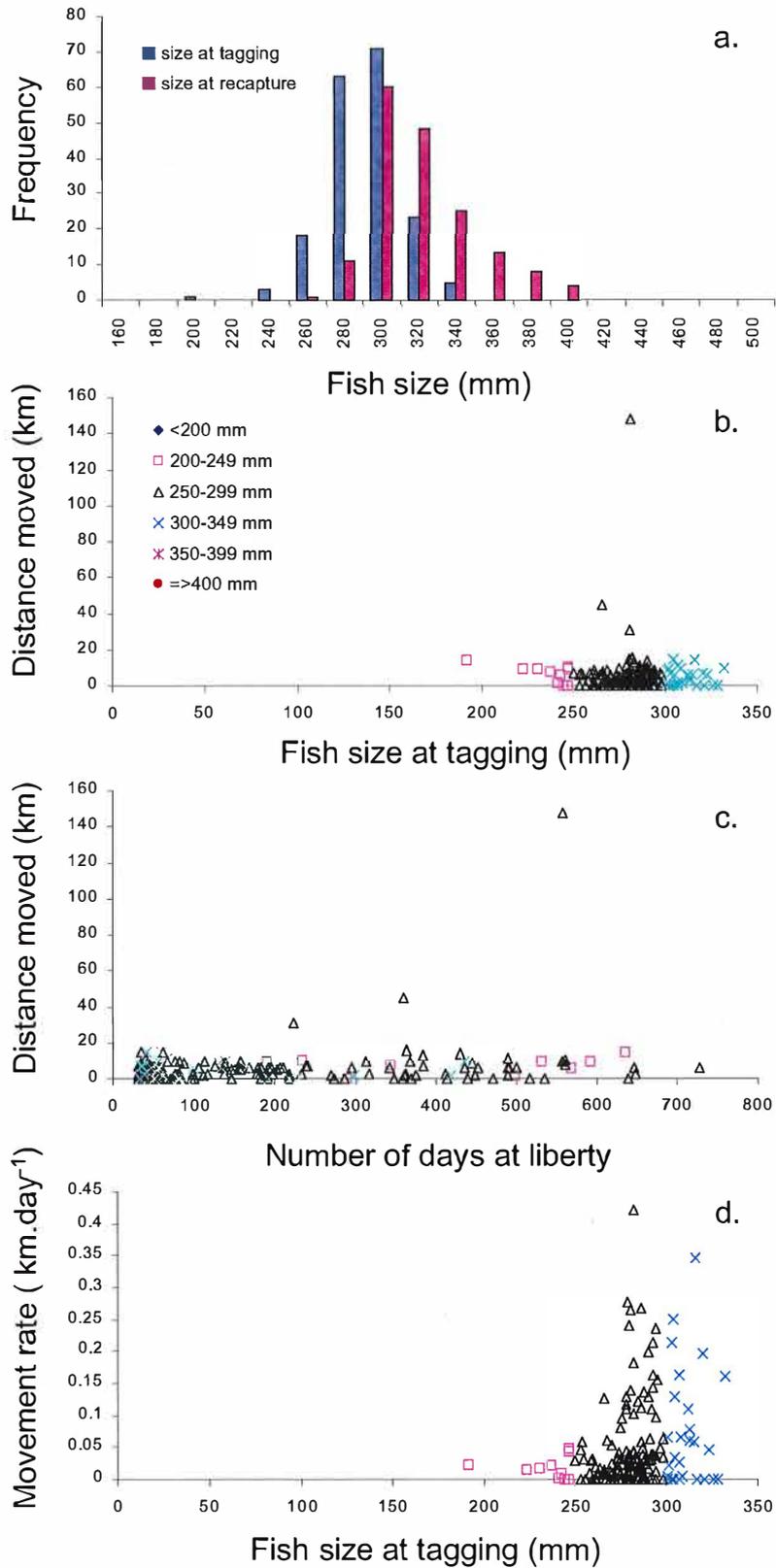


Fig. 6.9 Characteristics of fish movement from fish tagged in Baird and Venus Bays. a. Frequency distributions of tag and recapture sizes. b. Relationship between distance moved and size at tagging. c. Relationship between distance moved and time at liberty. d. Relationship between rate of movement and size at tagging.

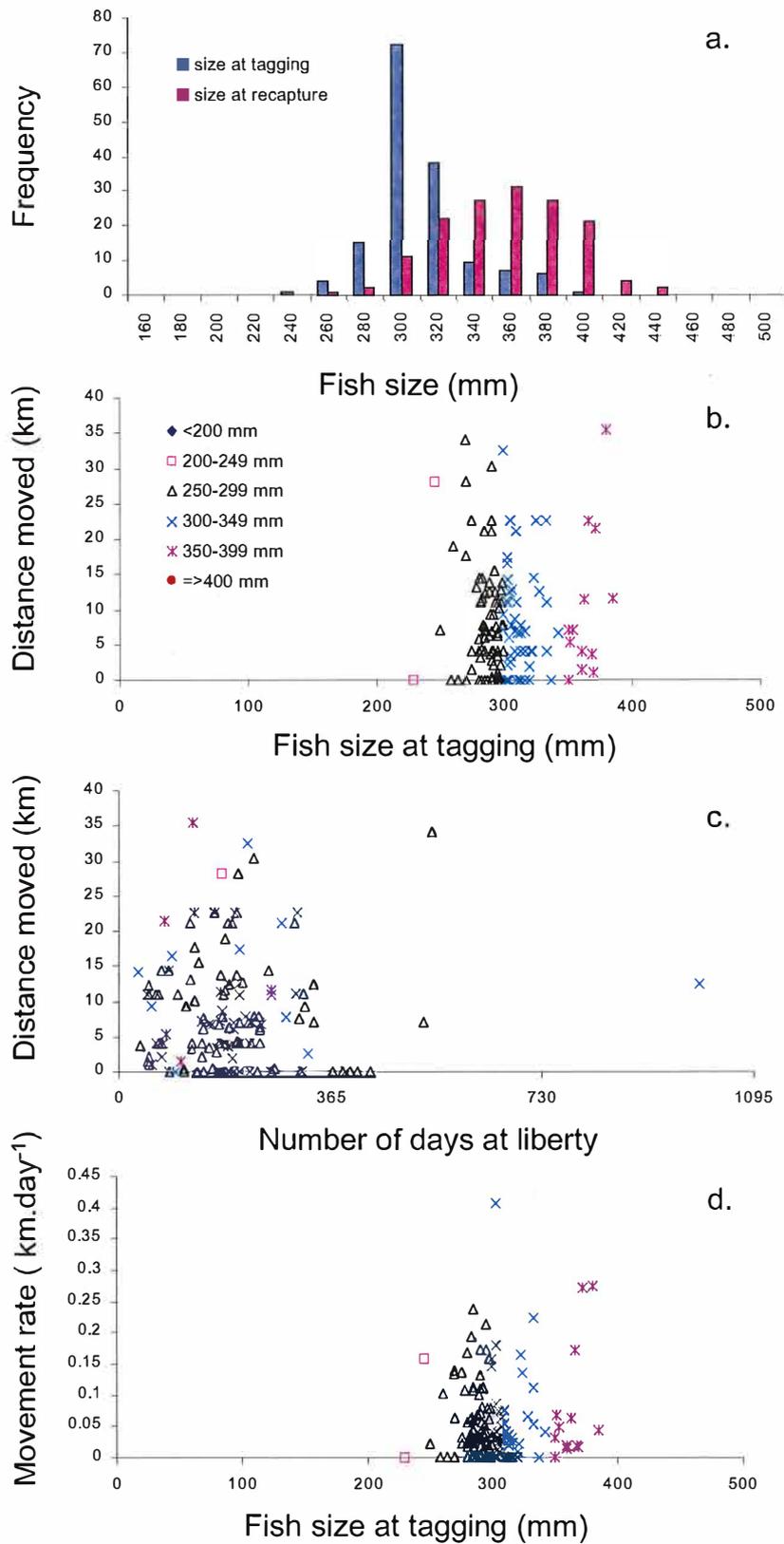


Fig. 6.10 Characteristics of fish movement from fish tagged in Denial Bay. a. Frequency distributions of tag and recapture sizes. b. Relationship between distance moved and size at tagging. c. Relationship between distance moved and time at liberty. d. Relationship between rate of movement and size at tagging.

6.4 Discussion

This study has served to indicate the potential for movement by King George whiting, and the size and age at which they are capable of substantial movement. It determined that fish in the smallest size class considered (i.e. 200 – 249 mm TL) were generally not recaptured far from the tag site until after a considerable period. Alternatively, some in the 250-299 mm class were recaptured up to 60-100 km distance only 1-2 months after tagging and those >300 mm were capable of moving up to 200 km within only 1-2 months of tagging. Most fish were estimated at less than 3 –4 years old at recapture.

Although clearly King George whiting as young as 1 – 2 years have the potential for substantial movement, >50% of recaptures from the broad range of areas considered were made within only 10 km of the tag site (Fig. 6.11). This is despite that many fish were tagged for periods of months to years. Thus, despite the potential for movement, many fish did not in fact move far. Consequently, there is a broad range in the rates of movement from 0 – 2.5 km.day⁻¹.

Eastern Region

In Gulf St. Vincent, 72.6% of recaptures were made within 20 km of the tag site, whilst only 5% exceeded 100 km (Fig. 6.11). Many smaller movements were made along the coast that was nearest the tag site. Alternatively, the further recaptures generally reflected displacement to the south-west, some being found as far away as the north-west coast of Kangaroo Island.

In comparison, fish tagged in the north-east bays of Kangaroo Island presented a different picture of movement. Despite that many were tagged for >1 year, approximately 95% were recaptured within 20 km of the tag site. There was no apparent systematic, directional nature to their movement as was the case in Gulf St. Vincent. Several fish that moved the longest distances ended up along the north coast of the island.

The movement patterns identified here are compatible with the differences in size and age structures between Gulf St. Vincent and the north coast of Kangaroo Island (Chpt 3). Where the fished population from Gulf St. Vincent was dominated by 3 year olds (91.5%) and had a modal size of 320 mm TL, those from the north coast of Kangaroo Island ranged up to >500 mm TL in size and incorporated the age range of 3 – 17 years (Chpt 3). It would appear that fish leave the gulf and shallow bays of the island and eventually move to the more reef-dominated habitat of Investigator Strait and the north coast of the island where they can persist for numerous years. Also, this place where the older, larger fish are found is one of the few spawning grounds yet identified for this species in southern Australia (Chpt 4).

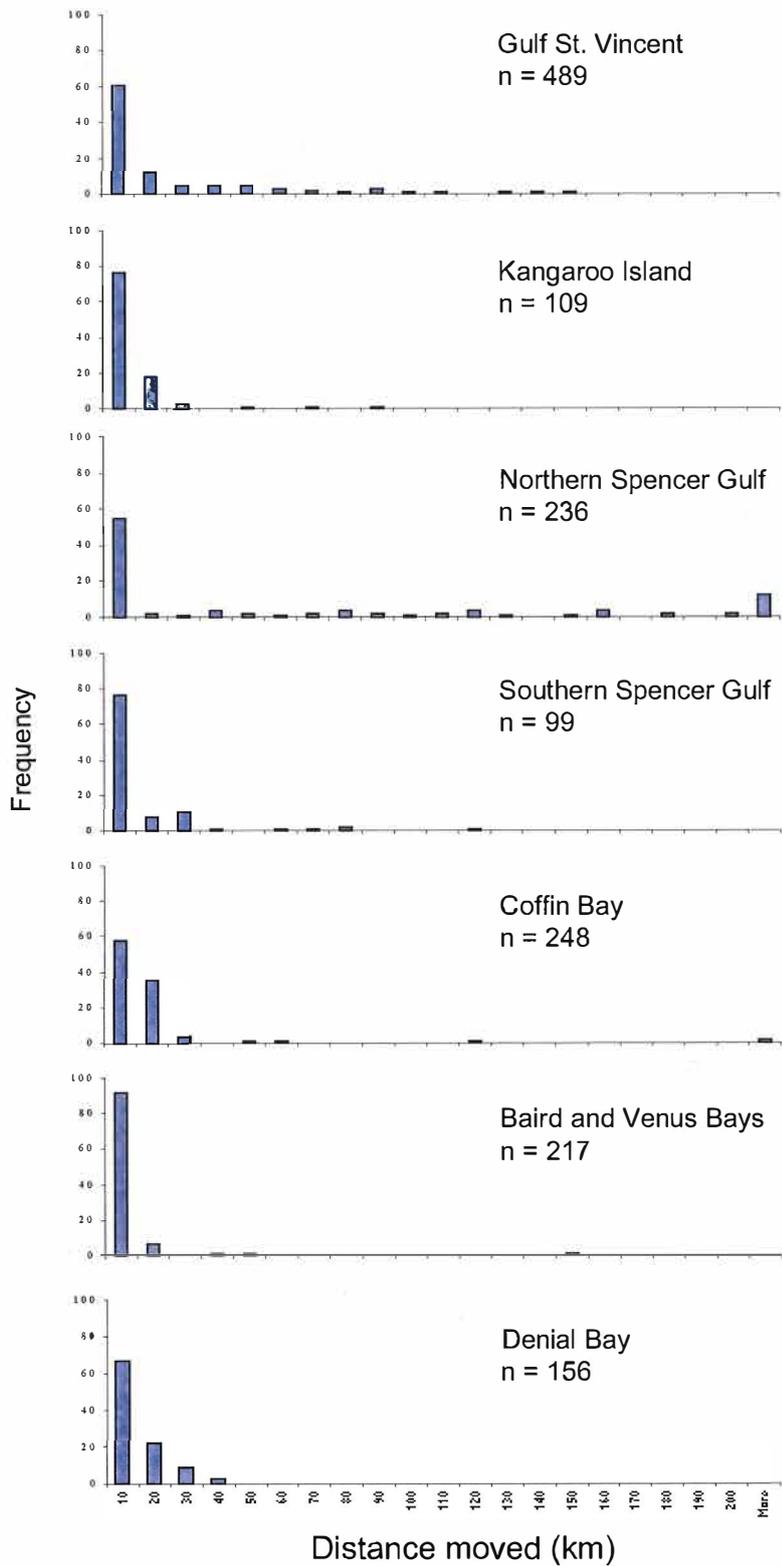


Fig. 6.11 Comparative summary of the frequency distributions of distances moved by fish tagged in each of the different areas (n = number of recaptures after >30 days at liberty and for which tag and recapture locations were known).

Spencer Gulf

Fish tagged in northern Spencer Gulf demonstrated the greatest tendency towards movement, and moved the largest distances. Although 54.5% of these fish moved <10 km, 12.3% were recaptured >200 km from the tag site. Movement was towards the south, but possibly because of the orientation of the gulf, the displacement was generally towards the south-west.

In contrast, movement in the southern part of the gulf was generally quite restricted. Approximately 94% of fish moved <30 km and only one fish moved more than 90 km. There was no systematic displacement in a particular direction.

These data indicate general net movement of fish from northern to southern coastal areas, but no reciprocal movement in the opposite direction. Such movement patterns could account for the north/south gradient in size and age structures. Fish caught in the north were mainly small and 2-3 years old, but in the south, fish were larger and the age structures were more complex with fish living up to 11 years (Chpt 3).

West Coast

Fish tagged in the west coast bays showed the least tendency for movement. A high proportion of recaptures from each of Coffin Bay, Baird and Venus Bays and Denial Bay (92.4, 98.7 and 88.5% respectively) were made within 20 km of the tag site. Despite that most fish were recaptured within the bay where they were initially tagged, a very small percentage made substantial movements along the west or north-west coasts of Eyre Peninsula.

Tag/recapture data from this region were less informative than for the two former regions. Since most recaptures were made within or in the vicinities of the bays, these data cannot account for why the age structures of the fished populations are dominated by 3 year old fish (Chpt 3). Perhaps the older fish leave the bays and move off-shore to places that are not normally fished, and therefore provide no opportunity for recaptures.

Inter-regional Movement

There was little evidence of movement between the three main regions. In total 1,589 recaptures from the three regions provided information on movement patterns. Of these, only 5 fish moved between regions. One fish from Gulf St. Vincent and two from Spencer Gulf moved to Coffin Bay, and two fish moved from Coffin Bay to Spencer Gulf. Although such a low rate of exchange of individuals

would help maintain genetic homogeneity (Chpt 7), from a fishery perspective it may be best to consider the post-settlement populations of King George whiting of the three regions as discrete population units.

6.5 References

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CHAPTER 7. STOCK STRUCTURE BASED ON ANALYSIS OF MITOCHONDRIAL DNA AND MICROSATELLITES.

L.J. Haigh, S. Donnellan

7.1 Introduction

There are a number of factors related to the life history and habitat of King George whiting that may influence the stock structure. Spawning appears to be restricted to specific off-shore locations (Fowler et al. 1999, Fowler et al. 2000), while larvae are advected between spawning grounds and nursery areas and early post-larval development occurs in shallow sea grass beds (*Zostera* and *Heterozostera* spp.) or bare sand (Fowler and Short 1996). The eggs are planktonic and after hatching, larvae maintain a long larval duration relative to other species of marine teleosts. In South Australia, it ranges from 79 to >130 days, increasing systematically through the settlement season (Fowler and Short 1996), while in Victoria, it ranges from 100 to 170 days (Jenkins and May 1994). The long larval duration provides opportunity for advection over long distances by hydrographic processes, which may facilitate gene flow between geographically distant populations and significantly influence the stock structure.

Previous investigation of stock structure for King George whiting has been limited to two pilot allozyme studies that failed to identify sufficient polymorphic loci (Dixon et al. 1987, Donnellan unpubl. data). Here, we report a study in which two independent molecular techniques, mitochondrial DNA (mtDNA) analysis and nuclear DNA microsatellite polymorphism, were used to test the null hypothesis of panmixia for the King George whiting populations across southern Australia. The combination of mitochondrial and nuclear markers should provide information about both long and short-term gene flow as each type of marker can respond to changes in population demographic parameters at different rates. For the mitochondrial analysis, we phylogenetically analysed sequences from part of the control region, the major non-coding region of the vertebrate mitochondrial genome, from five or more individuals from eight representative areas. This approach provides a phylogeographic perspective relevant mostly to historical population processes. In contrast, microsatellites are subject to rapid mutation rates and combined with their bi-parental mode of inheritance provide information relating to more recent influences on gene flow. Nine polymorphic microsatellite loci, isolated from KGW, were used to assess population differentiation in allele frequencies across the geographic range of the species. This approach generates allele frequency data that mainly address recent population processes and short-term management issues.

7.2 Materials and methods

Tissues and DNA extraction

Tissues used in this study were either liver samples from adults, or whole juvenile fish collected from across the geographic range of the species. Samples were collected from different locations in Western Australia, South Australia and Victoria. Locations, collection dates and sample sizes are listed in Table 7.1. The confamilial, *Sillago schomburgki*, was used as an outgroup for the mitochondrial DNA study.

Table 7.1. Details of King George whiting sampled for mitochondrial DNA (mtDNA) and microsatellite (nDNA) analysis. ¹ population code in parentheses, GSV = Gulf St Vincent, SG = Spencer Gulf, WC = West Coast of South Australia. ² Ad = adult, Juv = juvenile.

Sample location ¹	Latitude (S)	Longitude (E)	Date	Age ²	Sample number	
					mtDNA	nDNA
Barker Inlet 1 (BI1) GSV	34 47	138 32	10/1993	Juv	19	30
Barker Inlet 2 (BI2) GSV	34 47	138 32	11/1989	Juv	-	30
Port Vincent (PV) GSV	34 47	137 51	11/1993	Juv	-	33
Franklin Harbour (FH) SG	33 43	136 57	9/1994	Juv	15	30
Louth Bay (LB) SG	34 33	135 36	4/1991	Ad	5	-
Wedge Island (WI) SG	35 09	136 27	10/1992	Ad	1	-
Thistle Island (TI) SG	35 00	136 09	4/1996	Ad	-	30
Streaky Bay (SB) WC	32 35	134 05	10/1993	Juv	17	25
Cape Jaffa (CJ) SA	36 57	139 40	2/1997	Ad	-	31
St Leonards (SL) Port Phillip Bay VIC	38 10	144 45	3/1992	Ad	6	33
Western Port (WP) VIC			10/1995	Juv	11	21
Corner Inlet (CI) VIC	38 47	146 30	1/1992	Ad	6	-
Nornalup Inlet (NI) WA	35 00	116 44	10/1992	Ad	-	25
Shoalwater Bay (SB) WA	32 15	115 44	4/1994	Ad	22	-

The tissues were either frozen in liquid nitrogen then stored at -80°C or preserved in ethanol/ sodium chloride solution 1:1 at room temperature. DNA was extracted from the tissues using either phenol/ chloroform (Sambrook et al. 1989) or salt extraction (Miller et al. 1988) methods, followed by ethanol precipitation then resuspended in nuclease free water.

Mitochondrial DNA

A 350 bp fragment of control region mtDNA was PCR amplified using the primers MT15996L (5'-CTCCACCATCAGCACCCAAAGC-3' designed by M. Elphinstone, Southern Cross University) and MT16498H (5'-CCTGAAGTAGGAACCAGATG-3' Meyer et al. 1990). Amplification conditions were: 50-100 ng target DNA, 10 pmol each primer, 0.2mM each of dATP, dTTP, dCTP and dGTP, 4mM MgCl₂, 1x Taq dilution buffer and 0.75unit Promega Taq DNA polymerase in a 50µl reaction volume. PCR cycling conditions were: 94 °C 3', 55 °C 45'', 72 °C 1' for one cycle, 94 °C 45'', 55 °C 45'' 72 °C 1' for 34 cycles and 72 °C 6', 26 °C 10'' for one cycle (FTS-320 Thermal Sequencer, Corbett Research). PCR products were purified using Bresa-clean Nucleic Acid Purification Kit (Bresatec). Both strands of the purified PCR product were sequenced with the same primers used for PCR with the Perkin Elmer ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit. Products were run on an ABI 373 or 377 model auto sequencing machine.

To test whether the control region primers amplified nuclear paralogous sequences, a common problem when using total cellular DNA as a PCR template (Zhang and Hewitt 1996), we carried out the following protocol of Donnellan et al. (1999). "Purified" mt DNA was prepared on a caesium chloride gradient according to the protocols of Dowling et al. (1996). Serial dilutions (eg. neat to 10⁻⁶) of the "purified" mtDNA were amplified with three sets of PCR primers: G71 (TCCGGTYGATCCTGCC) and G72 (CTGGAATTACCGCGGCTGCT) (designed by P. Monis) specific for the nuclear locus *18S rRNA*, L1091/H1478 specific for *12S rRNA* (Kocher et al. 1989), and the control region primers being tested. For each primer pair, we determined the maximum dilution (the endpoint) that produced successful amplification. In practice, it was usual to observe a thousand fold difference between the end points for the *12S rRNA* primer pair and the *18S rRNA* primer pair. Either of two outcomes were observed for the mitochondrial test primer pair. If the mitochondrial test primers and *12S rRNA* primers amplified to a similar endpoint that was more dilute than for the nuclear primers, we concluded that the product was derived from mtDNA. The test primers may, however, be able to amplify a nuclear paralogue as well as the true mitochondrial product when used with total cellular DNA. To test this, we compared the sequence of the product amplified from the maximum dilution of the enriched mtDNA with that from total cellular DNA from the same individual. If these sequences were the same, we concluded that the primers only amplified mtDNA. If the sequences were different however, the primers may also have amplified nuclear DNA. If this occurred we would design new primer pairs and test their ability to amplify only mtDNA by the procedure described here. If the endpoint for the test primers was the same endpoint as the *18S rRNA* primer pair, we would conclude that a nuclear paralogue could have been amplified. In this case, new primers would need to be designed and tested for their ability to amplify mtDNA only.

The sequences were aligned with Clustal W (Thompson *et al.* 1994) using default settings and were analysed using a variant of the maximum likelihood approach, quartet puzzling (QP) and distance based methods in PAUP* 4d65 written by D. Swofford. Haplotype frequency data were analysed using analysis of molecular variance (AMOVA) implemented in the Arlequin package (Schneider *et al.* 1997).

Microsatellites

Microsatellite markers were isolated from KGW using two different methods, a version of the PCR-based procedure of Grist *et al.* (1993) modified by (Cooper *et al.* 1997) and magnetic bead enrichment (Gardiner *et al.* 1999). In each case, (AAAG)₆ probes were used to isolate tetranucleotide repeat loci. A total of 32 clones were isolated by the first method and partially sequenced with the Sp6 vector primer using Perkin Elmer ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit with the products run on an ABI 373. Twenty-four of these appeared to have an insert containing AAAG repeats. Pairs of specific primer were then designed targeting the unique flanking regions of each repeat region. Ten complete microsatellite markers and their flanking regions were amplified and fully sequenced while the remaining 14 were discarded due to poor amplification or sequencing results. The second isolation method yielded 18 positive colonies and nine were shown to contain repeat DNA following sequencing. Specific primers were designed targeting the flanking regions in each (Table 7.2).

A total of 18 loci were isolated and tested for polymorphism in a panel of ten KGW genomic DNA samples from across the geographic range. Markers were amplified using 50-100 ng target DNA, 10 pmol each primer, 0.2mM each of dATP, dTTP, dCTP and dGTP, 4mM MgCl₂, 1x Taqgold *dilution buffer and 0.5unit Promega Taq Gold DNA polymerase in a 25µl reaction volume. PCR cycling conditions were: 94 °C 3', 58 °C 45'', 72 °C 1' for one cycle, 94 °C 45'', 58 °C 45'' 72 °C 1' for 34 cycles and 72 °C 6', 26 °C 10'' for one cycle. Products were electrophoresed on 6% non-denaturing polyacrylamide gels. Nine markers were polymorphic in the samples tested. A single primer from each pair was re-synthesised and labelled with ABI fluorescent dyes. The population sub-set (s) described in Table 7.1 were then genotyped for each marker using the Gene Scan automated Genotyper system (ABI GeneScan).

Table 7.2. Microsatellite sequences and PCR primers for the nine King George whiting microsatellite loci (the PCR annealing temperature was 58°C for each locus).

Locus	Microsatellite sequence	Primer
Sp2	(ATAG) ₈ (AAAG) ₅	5'-ATGCGTGAAGATGGTGTCA 5'-CTGTTCTCAGCAGTGCTTCA
Sp7	(AAAG) ₇	5'-AAGCTCATTTTCATCAGCGT 5'-CGGATCGGAATTTGAAGACA
Sp19	(AAAG) ₄	5'-CGTGTAACCCAGAAACCTACT 5'-CATCGAAGCATTGCCTGTAA
Sp22	(AAAG) ₇	5'-CTACTTCACTGCTGCACTCACA 5'-GGACCAACACAAGACACACAA
Sp32	(AAAG) ₄ (ACAG)(AAG) ₃	5'-ACACAGATCGCGCACTTGTA 5'-CACTGTCCTCGCTGTGGTGA
Sp35	(AAAG) ₄	5'-TCCTAGCTACGATGATGGATG 5'-TCTGGTCAGATTCGTCGATGG
Sp36	(AAAG) ₆	5'-CCTCAGTAAGCGCCAGTAATAGAC 5'-CCTACAGCGATTGGTACAGCAC
Sp38	(CCT) ₈	5'-CCGTGACCGGTTCCATTGAG 5'-TCCTCAACTGCGTCTGTGTTCA
Sp39	(GTATC) ₁₁	5'-TTGCTGACCATGTCAAGTTGA 5'-CACCAGGACAAGGCTGATATG

Data analysis: intrapopulation

The number of alleles per population and overall, and observed heterozygosity were calculated with the program GENEPOP, version 3.1b (Raymond and Rousset 1995). Non-parametric exact significance testing methods were used to evaluate conformance to linkage and Hardy-Weinberg genotypic equilibria. When less than five alleles were present at a locus an exact test was performed, for loci with larger numbers of alleles unbiased estimators of exact significance probabilities were calculated using the Markov chain algorithm of Guoy and Thompson (1993) for testing linkage equilibria, Hardy-Weinberg equilibria, and population differentiation. Tests were performed with the program GENEPOP version 3.1b, with a Markov chain length of 500,000 steps (Raymond and Rousset 1995). Type 1 error was controlled with the Bonferroni method (Rice 1989).

Data analysis: interpopulation

The significance of allele frequency differences between populations was assessed using the exact tests in the program GENEPOP, version 3.1, and the significance level was determined after 50 batches of 100 000 iterations each. The genetic variance of population structure was determined using two models: the infinite allele model F_{ST} (Weir and Cockerham 1984) and the step-wise mutation model R_{ST} (Slatkin 1995). F_{ST} was calculated using the program ARLEQUIN, version 1.1 (Schneider et al. 1997), and the significance level for the overall values was determined after 10000

iterations and for the population pairwise values after 992 permutations. An unbiased version of R_{ST} (designated R_{ST}/std), in which allele sizes are transformed to standardised variances, was calculated using the program RST CALC, version 2.2 (Goodman 1997), and significance levels were determined after 100 permutations. An isolation-by-distance model was tested by regressing the \log_{10} values of the population pairwise estimate of the overall number of migrants per generation (Nm) against the \log_{10} of the population pairwise geographical distance values (Slatkin 1993), and where:

$$Nm = 1/4(1/X_{ST} - 1)$$

and where X_{ST} is either F_{ST} or R_{ST}/std . Prior to calculating Nm , all negative X_{ST} values were changed to 0.0001. The significance of the regression was determined after 10000 permutations of a Mantel procedure to assess the correlation between $\log_{10}Nm$ and \log_{10} distance. The regression and Mantel test were performed using the program GENEPOP, version 3.1b. An unrooted phylogram of population pairwise genetic distances was constructed using the neighbour-joining method (NJ) (Saitou and Nei 1987), as implemented in the program PHYLIP, version 3.57c (Felsenstein 1993). The genetic distance developed for the stepwise mutation model, $\delta\mu^2$ (Goldstein et al 1995), was used to estimate the genetic distances between populations. The $\delta\mu^2$ distance was obtained from the program RST CALC version 2.2 (Goodman 1997).

7.3 Results

Mitochondrial DNA

As a comparison of sequences from total cellular and purified mitochondrial DNA templates of one individual showed no evidence of paralogous sequences, the remaining 103 samples were sequenced from total cellular DNA templates. Sequences of 504 nucleotides of the 5' end of mitochondrial control region were determined from samples from eight areas (Table 7.1). Among the 105 individuals sequenced, there were 82 unique haplotypes and 11 of these were shared between two or more individuals. One haplotype, 8, was found in nine individuals from across the species range. The haplotype diversity within areas was high, ranging from 0.95-1.0. Nucleotide diversities were low, ranging from 0.024 to 0.034. Jukes-Cantor distances from the outgroup to the ingroup sequences ranged from 0.57 to 0.64.

As the number of parsimony informative sites was low (149 sites) relative to the number of haplotypes (82), we used distance-based and maximum likelihood (ML) approaches to explore relationships among haplotypes. An ML estimate of the transition to transversion ratio (ts/tv) was 3.196 and maximum Jukes-Cantor distances between sequences of the ingroup were 0.064. Under these conditions the Kimura 2-parameter distance to estimate divergence between sequences is recommended. The neighbour-joining algorithm was used to construct a tree of relationships among the control region haplotypes from the Kimura 2-parameter distances (Fig. 7.1a). A version of the maximum likelihood criterion of optimality, quartet puzzling (QP), was used as it is computationally less intensive than the usual implementation of this criterion (Strimmer and von Haeseler 1996). The quartet puzzling option in PAUP* 4.0d65 was used with 1000 puzzling steps (Fig. 7.1b).

It is apparent from an examination of the NJ and QP trees that little strongly supported structure is present among the KGW haplotypes. Only seven nodes in the NJ analysis received strong support from 2000 bootstrap pseudoreplicates (>70%). While the QP tree shows a larger number of nodes with high reliability values, caution should be exercised in equating reliability values directly with bootstrap proportions (Cao et al. 1998). Apart from poorly resolved topological structure, the tree is a relatively shallow one, ie low nucleotide divergences among haplotypes and few if any clearly distinct lineages. The correspondence between geographical origin of samples and their position in the tree is also without any structuring. For instance the haplotypes observed among the 17 individuals from Streaky Bay (SB) are distributed throughout the tree, a similar pattern is apparent for all sampled localities, ie haplotypes from single localities or regions do not form discrete clusters in the tree.

Haplotype frequencies were compared among regions, by pooling samples into the following

categories: **WA** – SWB, **WC** – SB, **SG** – FH, LB, WI; **GSV** – BII; **VIC** – CI, SL, WP. Table 7.3 summarises the within-region nucleotide diversity, nucleotide divergence between regions and the proportion of variance distributed between regions. The majority of genetic variance is distributed within regions (99.26%) and a small fraction between regions (0.74%), an overall $\phi_{ST} = 0.00743$ ($P < 0.18$).

Table 7.3. Statistical analysis of mitochondrial control region nucleotide sequence variation among samples of KGW from five regions.

Figures below the diagonal are nucleotide divergence, those on the diagonal (in bold) are within population nucleotide diversity, and those above the diagonal are the proportion of variation distributed between regions (ie ϕ_{ST}). The significance of ϕ_{ST} value is indicated as *** $P < 0.001$, ** $P < 0.01$ or * $P < 0.05$.

	<i>n</i>	VIC	GSV	SG	WC	WA
VIC	23	0.0347	0.0365	0.0285	0.0000	0.0000
GSV	19		0.0267	0.0148	0.0098	0.0000
SG	21			0.0270	0.0040	0.0073
WC	19				0.0343	0.0000
WA	23					0.0327

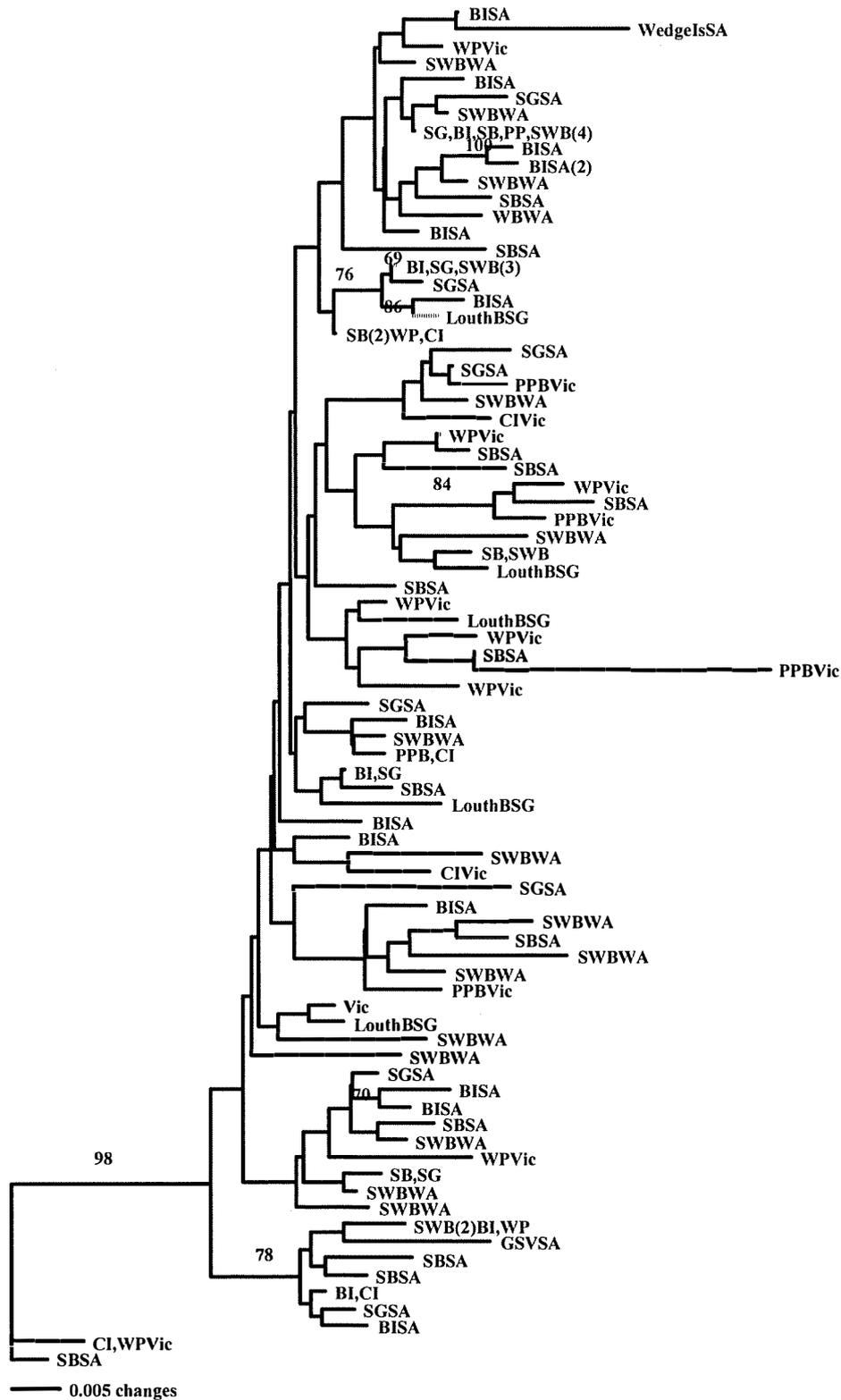


Fig. 7.1a Neighbour-joining (NJ) phylogram of evolutionary relationships among 105 King George whiting mitochondrial control region haplotypes. Numbers at nodes represent NJ bootstrap proportions from 2000 pseudoreplicates.

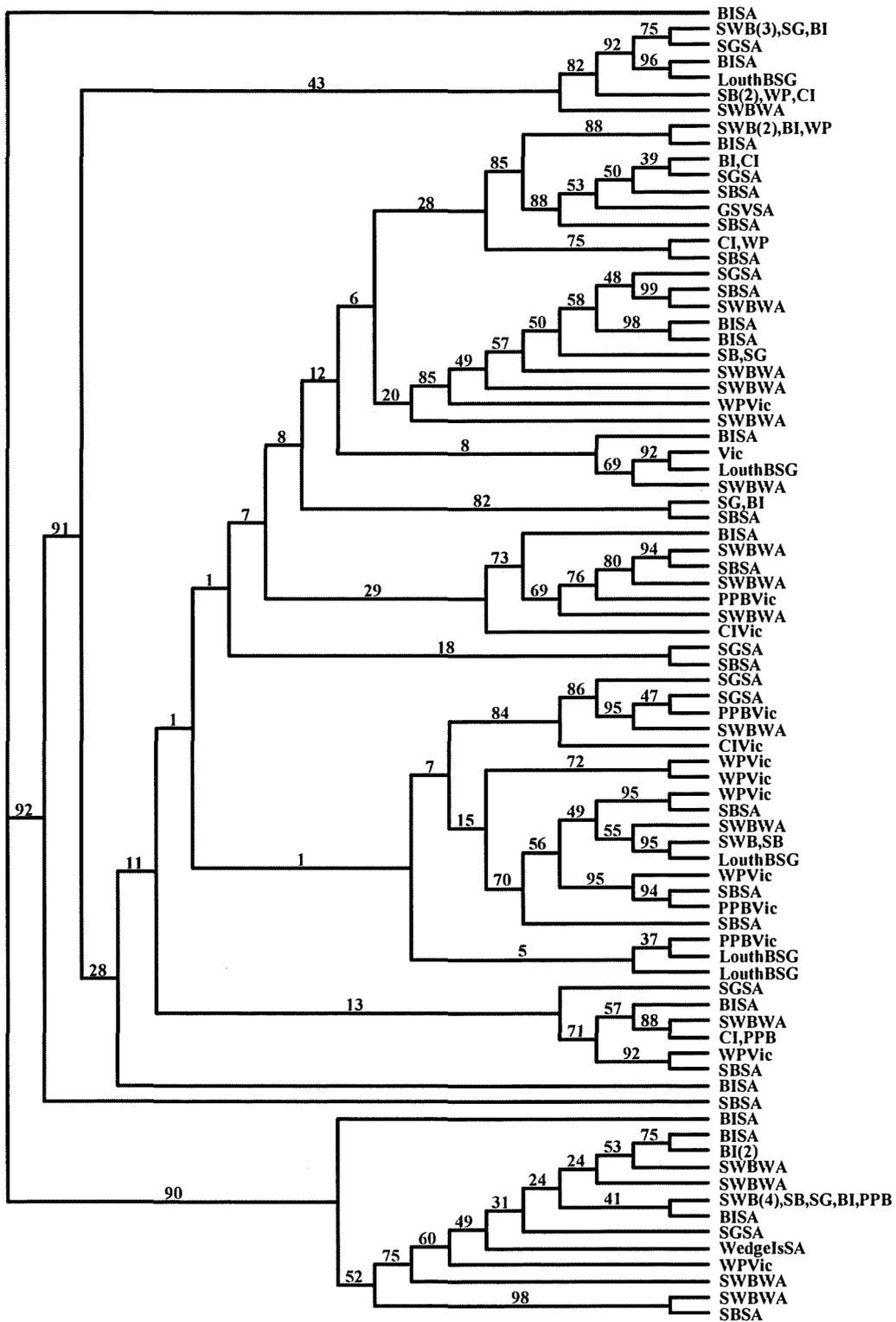


Fig. 7.1b. Quartet puzzling (QP) tree of evolutionary relationships among 105 King George whiting mitochondrial control region haplotypes. Numbers at nodes represent QP reliability values.

Microsatellites

Genotypes of up to 288 individuals from ten locations were scored for 9 microsatellite loci. The number and the size range of alleles at each locus and observed heterozygosities (H_o), for each population, are presented in Table 7.4. Allele frequencies are presented in Appendix 1.

Population analysis

Inspection of the genotype arrays showed, that for locus Sp38, a small number of individuals that had been typed as homozygous for rare alleles. These individuals came from four populations that otherwise contained only one other common allele. In view of these potentially anomalous typings and the high frequency of the common allele, either fixed or $p > 0.99$, the locus was omitted from further consideration. Tests for linkage equilibrium on the remaining eight loci produced only one significant test after Bonferroni adjustment of significance level to 0.001 (0.05/36), for locus Sp7 and Sp22 in the FH population ($P < 0.0001$). Tests for conformity to Hardy-Weinberg proportions produced, after Bonferroni adjustment, significant results for locus Sp39 in all populations. The presence of null alleles (usually due to non-amplification of certain alleles) is a relatively common phenomenon in PCR based microsatellite analyses (Pemberton et al. 1995). In view of the likelihood of the presence of null alleles, locus Sp39 was omitted from further analysis. Significant departures from Hardy-Weinberg proportions were observed in two of the remaining 70 tests; for locus Sp22 in population WP ($P = 0.0007$) and locus Sp32 in population NI ($P = 0.0044$), after Bonferroni adjustment of significance level to 0.005 (0.05/10). A total of 77 alleles were observed among the seven remaining loci. The total number of alleles detected in a single population varied from 35 in SB and TI to 45 in BI1 (Table 7.4). Observed heterozygosities (H_o) ranged from 0.12 (locus Sp36) to 0.96 (locus Sp22). Mean observed heterozygosities per locus ranged from 0.239 (Sp36) to 0.774 (Sp22) (Table 7.4).

Significant exact tests for genetic differentiation between populations with the remaining seven loci are presented in Table 7.5. Most pairwise population comparisons were not significant at any locus. Apart from the BI1/PV comparison the other four pairwise comparisons with significant test values involved single loci only. For the BI/PV comparison two loci showed significantly different allele frequencies. These population samples were collected approximately 70 km apart within the Gulf of St Vincent.

Pairwise F_{ST} and R_{ST}/std values between populations are presented in Tables 7.6 and 7.7 respectively. Both measures had similar proportions of negative values (16 and 14 respectively), while six pairwise F_{ST} comparisons and eight pairwise R_{ST}/std comparisons were significantly different from zero.

Significant values from both measures had similar ranges, F_{ST} : 2.0 to 5.3%, R_{ST}/std : 1.8 to 5.8%. Populations appearing most frequently among the significant comparisons differed between the two measures, with only the SL population appearing several times in both measures.

The mean N_m estimated from R_{ST}/std was 9.1322 and from Slatkin's (1985) private allele method was 9.7108. Pairwise migration levels were narrowly variable (Table 7.8), N_m ranging from < 1.0 to 286. A test of isolation by distance resulted in the following regression equation for R_{ST}/std $\log_{10}N_m = 0.469 + 0.545(\log_{10}distance)$. The correlation between $\log_{10}N_m$ and $\log_{10}distance$ was not significant for R_{ST}/std ($P = 0.16$). The unrooted phylogram in Fig. 7.2 shows no obvious geographical structure.

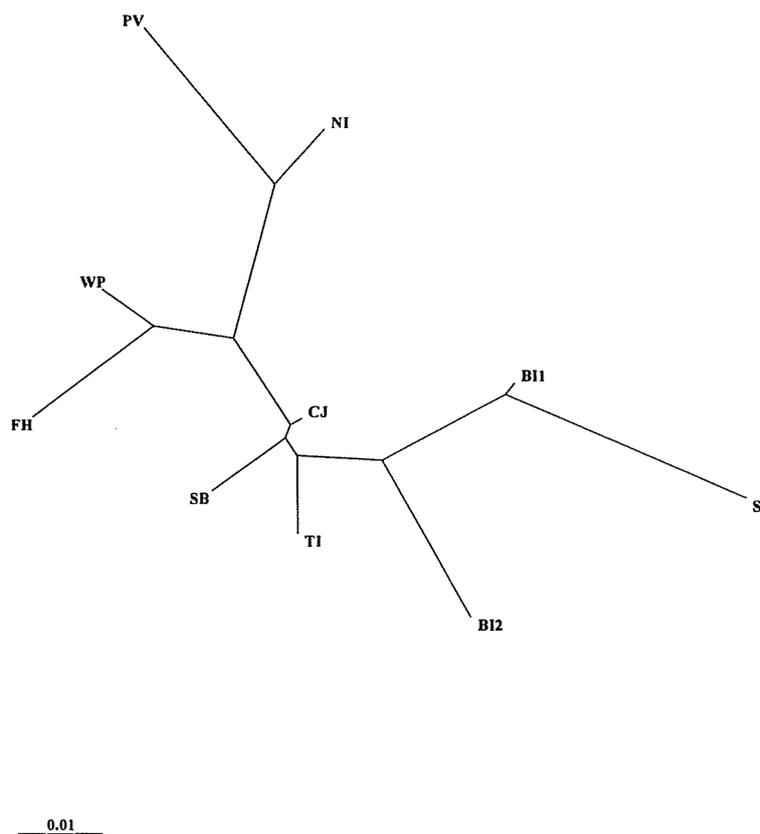


Fig. 7.2 An unrooted phylogram produced by the neighbour-joining algorithm from the $\delta\mu^2$ distance. Population codes are listed in Table 7.1.

Table 7.4. Sample number, observed allele number, allele size range and heterozygosity for the nine microsatellite loci in ten King George whiting populations.

Locus	BI1	FH	PV	SL	BI2	CJ	NI	TI		
SB	WP									
Sp2 (Mean H_0 = 0.671)										
N(sample)	28	30	24	26	29	28	24	30	25	21
N(allele)	11	17	12	13	11	14	12	10	10	13
Size rang	215-367271-375271-347271-355271-355271-367271-375271-339271-347271-391									
H_0	0.71	0.87	0.71	0.69	0.83	0.89	0.88	0.4	0.76	0.86
Sp7 (Mean H_0 = 0.466)										
N(sample)	28	28	29	30	30	32	25	30	25	19
N(allele)	4	5	6	7	5	4	4	5	4	4
Size rang	127-147119-147119-147119-147119-155119-147119-147119-147119-147119-147									
H_0	0.5	0.61	0.66	0.6	0.53	0.41	0.44	0.53	0.4	0.63
Sp19 (Mean H_0 = 0.361)										
N(sample)	26	26	29	29	30	32	25	30	25	21
N(allele)	3	2	2	2	2	2	2	2	2	2
Size rang	197-205197-201197-201197-201197-201197-201197-201197-201197-201197-201									
H_0	0.57	0.21	0.14	0.55	0.4	0.34	0.4	0.27	0.4	0.33
Sp22 (Mean H_0 = 0.774)										
N(sample)	26	30	22	22	28	31	23	30	25	21
N(allele)	17	11	14	10	15	16	12	11	12	13
Size rang	119-219139-187135-119135-187139-223127-219143-215143-219143-191131-191									
H_0	0.88	0.73	0.7	0.68	0.89	0.935	0.96	0.83	0.5	0.62
Sp32 (Mean H_0 = 0.363)										
N(sample)	31	30	33	33	28	31	24	30	25	20
N(allele)	3	2	2	2	2	2	2	2	2	2
Size rang	142-158150-158150-158150-158150-158150-158142-150150-158150-158150-158									
H_0	0.42	0.5	0.33	0.45	0.25	0.48	0.13	0.47	0.6	0.45
Sp35 (Mean H_0 = 0.438)										
N(sample)	31	29	33	30	26	31	25	30	25	20
N(allele)	5	3	3	3	3	4	5	3	3	3
Size rang	124-144128-140132-140132-140132-140124-140124-144132-140128-140136-144									
H_0	0.58	0.45	0.3	0.37	0.35	0.58	0.44	0.5	0.36	0.45
Sp36 (Mean H_0 = 0.239)										
N(sample)	31	30	32	31	29	32	25	30	25	21
N(allele)	2	2	3	2	2	2	3	2	2	2
Size rang	114-118114-118106-118114-118114-118114-118114-118102-118114-118114-118114-118									
H_0	0.35	0.33	0.09	0.32	0.24	0.19	0.12	0.23	0.38	0.14
Sp38 (Mean H_0 = 0.019)										
N(sample)	31	30	31	29	27		24	28		
N(allele)	2	2	2	2	2	1	2	3	1	1
Size rang	274-277277-280277-283277-280280-283	277	277-280274-280							
H_0	0.03	0.03	0.06	0	0	0	0	0.07	0	0
Sp39 (Mean H_0 = 0.434)										
N(sample)	31	29	32	33	25	25	25	29	24	19
N(allele)	12	12	10	10	9	9	8	10	13	13
Size rang	206-276206-276206-256206-281206-251206-261206-276206-266206-286201-276									
H_0	0.61	0.55	0.56	0.52	0.24	0.32	0.32	0.206	0.38	0.63

Table 7.5. Significant exact tests for genetic differentiation between populations and regions of King George whiting.

Numbers are number of tests that were significant at 0.05 level of significance before Bonferonni adjustment, Nominated loci are those etas significant after the significance level was adjusted to 0.001 (0.05/45 per locus) for populations and to 0.003 (0.05/15) for regions. * = P < 0.001, ** P < 0.0001.

(A) Population pairwise comparisons

	WP	SL	CJ	BI1	BI2	PV	FH	TI	SB	NI
WP	-									
SL	-	-								
CJ	-	-	-							
BI1	2	1	2	-						
BI2	1	1	1 Sp35 **	1	-					
PV	-	-	-	2 Sp2 * Sp19 *	2	-				
FH	-	1	-	2	1 Sp35 **	1	-			
TI	-	1	-	2	1 Sp35 **	1	1	-		
SB	-	-	-	1	1	1	-	1	-	
NI	-	-	-	2 Sp2 *	1	2	-	-	-	-

(B) Regional pairwise comparisons

	VIC	CJ	GSV	SG	SB	WA
VIC	-					
CJ	-	-				
GSV	1	1	-			
SG	1	-	2	-		
SB	1	-	-	-	-	
WA	1	-	1	2	-	-

Table 7.6. Matrix of pairwise F_{ST} values

* significantly different from zero at significance level of 0.05, from 10100 permutations

	WP	SL	CJ	BI1	BI2	PV	FH	TI	SB	NI
WP	-									
SL	0.01750	-								
CJ	-0.00577	0.02215*	-							
BI1	0.03430*	0.00496	0.01059	-						
BI2	0.02095	0.01337	0.00911	-0.00259	-					
PV	0.01297	0.05307*	-0.00071	0.04120*	0.00563	-				
FH	-0.00249	0.01083	-0.00826	0.00317	0.00993	0.01094	-			
TI	-0.01582	0.01417	-0.01112	0.02081*	0.01031	0.00266	-0.00115	-		
SB	-0.00897	0.00567	-0.00760	0.00438	0.01166	0.00780	-0.01197	-0.00759	-	
NI	0.01375	0.02323*	-0.00431	0.00004	-0.01108	-0.00500	-0.00324	0.00691	0.00759	-

Table 7.7 Matrix of R_{ST}/std values averaged over loci

* significantly different from zero at significance level of 0.05, estimated from 100 permutations

	WP	SL	CJ	BI1	BI2	PV	FH	TI	SB	NI
WP	-									
SL	0.0187	-								
CJ	-0.0049	0.0213	-							
BI1	0.0091	-0.0003	-0.0033	-						
BI2	0.0148	0.0181*	0.0063	0.0054	-					
PV	0.0138	0.0584*	0.0089	0.0375*	0.0262*	-				
FH	-0.0091	0.0308*	0.0011	0.0137	0.0238*	0.0284*	-			
TI	-0.0037	0.0175	-0.0122	-0.0028	0.0094	0.0172	0.0164	-		
SB	-0.0019	0.0149	-0.0110	-0.0097	0.0113	0.0200	-0.0021	-0.0070	-	
NI	-0.0060	0.0315*	-0.0032	0.0119	0.0042	0.0020	0.0009	0.0067	0.0071	-

Table 7.8. Matrix of N_m values estimated from R_{ST}/std averaged over loci

	WP	SL	CJ	BI1	BI2	PV	FH	TI	SB	NI
WP	-									
SL	13.0950	-								
CJ	-51.2106	11.5126	-							
BI1	27.2343	-999.0121	-76.0508	-						
BI2	16.5881	13.5434	39.3906	45.9959	-					
PV	17.9264	4.0305	27.7280	6.4104	9.2990	-				
FH	-27.8395	7.8572	232.9325	17.9464	10.2391	8.5513	-			
TI	-67.0290	14.0745	-20.7509	-90.4872	26.3613	14.2982	15.0318	-		
SB	-128.7678	16.5449	-22.9312	-26.0124	21.9029	12.2732	-116.6391	-35.8056	-	
NI	-41.8467	7.6862	-77.6276	20.8433	58.8097	122.6690	286.8759	37.1671	34.7242	-

Regional analysis

Allele frequencies were compared among regions, by pooling the population samples into the following categories: NI; SB; **SG** – FH, TI; **GSV** – BI1, BI2, PV; **CJ**; **VIC** – SL, WP. Tests for conformity to Hardy-Weinberg proportions, after Bonferroni adjustment of significance level to 0.007 (0.05/7), produced significant results for GSV at locus Sp36 ($P=0.0068$), for SG at locus Sp7 ($P=0.0029$), for VIC at locus Sp22 ($P<0.0001$) for WA at locus Sp32 ($P=0.0044$) and locus Sp36 ($P=0.0051$).

Exact tests of differentiation between regions, after Bonferonni adjustment of significance level to 0.003 (0.05/15) per locus, did not produce any significant results for any region by region comparison. A high proportion of pairwise F_{ST} values between regions were negative (6 out of 15 comparisons), indicating that a substantial proportion of genetic variance was distributed within regions (Table 7.9). Only two comparisons were significantly differently from zero, those involved GSV/VIC and VIC/WA. Resulting estimates of migration rates were uniformly high (Table 7.10).

Table 7.9. Region pairwise F_{ST} values

*significant F_{ST} P values at significance level of 0.05, from 100 permutations.

	GSV	SG	VIC	CJ	WA	SB
GSV	-					
SG	0.00571	-				
VIC	0.01454*	0.00036	-			
CJ	0.00268	-0.00948	0.00747	-		
WA	-0.00977	0.00188	0.01520*	-0.00431	-	
SB	0.00503	-0.00925	-0.00345	-0.00760	0.00759	

Table 7.10. Matrix of M values ($M=2N_m$)

	GSV	SG	VIC	CJ	WA	SB
GSV	-					
SG	87.04012	-				
VIC	33.89888	1380.77405	-			
CJ	185.99623	inf	66.45840	-		
WA	inf	265.39542	32.40465	inf	-	
SB	98.82448	inf	inf	inf	65.38958	-

7.4 Discussion

In recent years, several studies have shown the usefulness of microsatellites and mitochondrial DNA for detecting population structure, providing more variable markers than traditionally used markers such as allozymes (eg Rico et al. 1997, Ruzzante et al. 1996, Tabata and Mizuta 1997, Perez-Enriquez and Taniguchi 1999). The levels of polymorphism found in the present study compare well with studies of other marine fish species (Tabata and Mizuta 1997, Perez-Enriquez and Taniguchi 1999). Indeed the variability observed for the King George whiting mitochondrial control region is extremely high. In contrast, the average observed heterozygosity for the seven microsatellite loci ranging from 0.239 to 0.774, while substantially higher than that observed for most allozyme studies, is at the low end of variability for microsatellite studies. However most microsatellite studies to date have relied upon dinucleotide microsatellite loci which may have an inherently higher mutation rate than the tetranucleotide markers used in the present study. At this time, few if any microsatellite studies of marine fish species have utilised tetranucleotide markers.

The phylogeographic analysis of the distribution of mitochondrial control region haplotypes showed no evidence of long-standing population structure. Because of the high haplotype diversity, relatively low nucleotide diversity and lack of well supported lineages in the haplotype evolutionary tree we were unable, with the technology available to us, to type large numbers of individuals for an analysis of haplotype frequency differences between population samples. However, the limited analysis of haplotype frequencies that we were able to perform, did not indicate any evidence of population differentiation between regions. The pattern of mitochondrial DNA diversity observed for King George whiting is consistent with that expected for a recently expanded population. Detailed statistical analysis and modelling could be performed to test this proposition using recently-developed models. .

Patterns of differentiation from the microsatellite analysis at the population level appeared chaotic. Furthermore, there was no significant relationship between genetic estimates of migration and geographic separation distance. While the temporally replicated samples (Barker Inlet) clustered in neighbour-joining analysis of genetic distances, neither of the geographical replicates within the Gulf St Vincent or Spencer Gulf clustered. Tests showed only weak genetic differentiation with only one comparison involving more than one locus. The regional analysis showed even less evidence of population structure for all measures of differentiation and high rates of migration were estimated among regions.

In conclusion, King George whiting show no evidence of long-standing population structure and little evidence of contemporary population differentiation. However the ability to detect interruptions to

gene flow on a contemporary time scale may be limited if the species is not in genetic equilibrium (mutation/drift).

Acknowledgments. We thank Pat Barton, and SARDI staff for the collection of fish, Ralph Foster for assistance in the laboratory and R. Slade for assistance with some of the computer programs used in the statistical analyses.

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CHAPTER 8. FISHERY TRENDS

A.J. Fowler

8.1 Introduction

The computer model proposed for King George whiting is a spatial model that will incorporate for a number of locations within three fishery regions information on the dynamics of the exploited stock. It is also a temporal one, simulating population processes with a monthly time-step, as well as incorporating inter-annual variability. The estimation model (WHITEST) will provide estimates of fishery and population parameters as well as model equations. Output from the model will be estimates of five Biological Performance Indicators:

1. recruitment (yearly)
2. exploitation rate (monthly)
3. fishable biomass (monthly)
4. egg production (yearly)
5. population numbers (monthly).

For each locality within each region, several population processes will be made explicit in the model by rate equations, which will be largely derived from population age structures:

1. cohort survival through each simulation year, declining by both natural mortality and fishing mortality from both the commercial and recreational sectors;
2. migration into and out from each locality, during the adult life-history stage;
3. growth which varies seasonally.

Validation of the population model will be done using an iterative approach which seeks to improve the model description of the population, until acceptable levels of agreement with observations of available statistics and the time series of catch, effort and CPUE data are attained. The commercial catch and effort data provide the only continuous time series of data for the King George whiting fishery. Although some information on catch and effort has been recorded since July 1976, a full dataset of targeted catch and effort by gear type was not recorded until 1983/84. Information from this time until the present is maintained in the Marine Scalefish catch and effort database (GARFIS) by SARDI Aquatic Sciences.

The recreational sector also makes a substantial contribution to the catch and effort in the King George whiting fishery. Unfortunately there is no time-series of data on catch and effort

for this sector, and our best information comes from an extensive two year SARDI/FRDC project (92/81) that provided estimates of the recreational catch of the marine boat fishers in the main fishery areas of South Australia through a complete annual cycle (McGlennon and Kinloch 1997). These data from the recreational sector were compared with those from the commercial fishery over the same period.

The objectives of this chapter were:

1. to summarise the time series of catch and effort data from the commercial fishery;
2. to provide a spatial summary of the catch and effort data from the recreational boat fishery for the 12 month period of April 1995 to March 1996;
3. to compare the relative catch and effort between the commercial and recreational sectors for the 12 month sample period.

8.2 Material and Methods

Commercial fishery

The commercial marine scalefishers of South Australia are obliged to provide information on their catch and effort at the spatial scale of Marine Fishing Areas (Fig. 2.1). However, for the purpose of this report this is too small a scale over which to examine overall trends in catch and effort, so data from some adjacent blocks were combined to provide summaries for seven fishery regions. The names of these regions and the blocks they incorporate are specified in Table 8.1 and shown on Fig. 8.1.

For each region, data are summarised for each calendar year between 1977 and 1998. The data extracted from the database included: total live weight, targeted live weight, non-targeted live weight, and fishing effort (fisherdays) for the three dominant gear types (handlines, haulnets, gillnets). For the gillnet and handline sectors, the non-targeted fishing effort was calculated from:

non-targeted effort = (targeted effort)*(non-targeted catch)/targeted catch. Targeted catch and effort and non-targeted catch and effort were combined appropriately to provide estimates of total catch and effort, and to be used to calculate CPUE.

The methods of reporting catch and effort by fishers who use hauling nets, with respect to specifying their targeted species, meant that catch, effort and CPUE had to be divided into three categories, which are each reported here separately. The three categories were:

1. when King George whiting was targeted;
2. when no species in particular was targeted, (i.e. “000” was recorded on the return), and King George whiting was caught;
3. when any other species was targeted, but King George whiting was taken as by-catch.

Recreational Fishery

This report provides a spatial analysis of the catch and effort data in the recreational boat fishery for the period of April 1995 – March 1996 (McGlennon and Kinloch 1997). The geographic range of this recreational boat survey was from Victor Harbor to Ceduna (including 80 boat ramps), which was divided into the three geographic regions of Gulf St. Vincent, Spencer Gulf and the west coast. Within each region a number of set circuits of boat ramps were surveyed using the “bus-route” method, which involved travelling amongst a pre-determined set of boat ramps and waiting at each ramp for a prescribed period. During the wait period, the number of boat trailers was counted providing an estimate of fishing effort, whilst fishers returning to the boat ramp were interviewed to provide estimates of catch. These data were ultimately used to derive estimates of total catch and effort, using the techniques outlined in McGlennon and Kinloch (1997).

Table 8.1 - Regions considered in the analysis of CPUE data, indicating the GARFIS blocks combined to form the particular regions.

Region name	Region number	Marine Fishing Areas (from Fig. 2.1)
Far West Coast (FWC)	01	07, 08, 09, 10
Mid West Coast (MWC)	02	15, 16, 17, 18
Coffin Bay (CB)	03	27, 28
Southern Spencer Gulf (SSG)	04	29, 30, 31, 32, 33
Northern Spencer Gulf (NSG)	05	11, 19, 20, 21, 22, 23
Gulf St. Vincent (GSV)	06	34, 35, 36, 40, 43
Kangaroo Island (KI)	07	39, 41, 42, 44, 48, 49

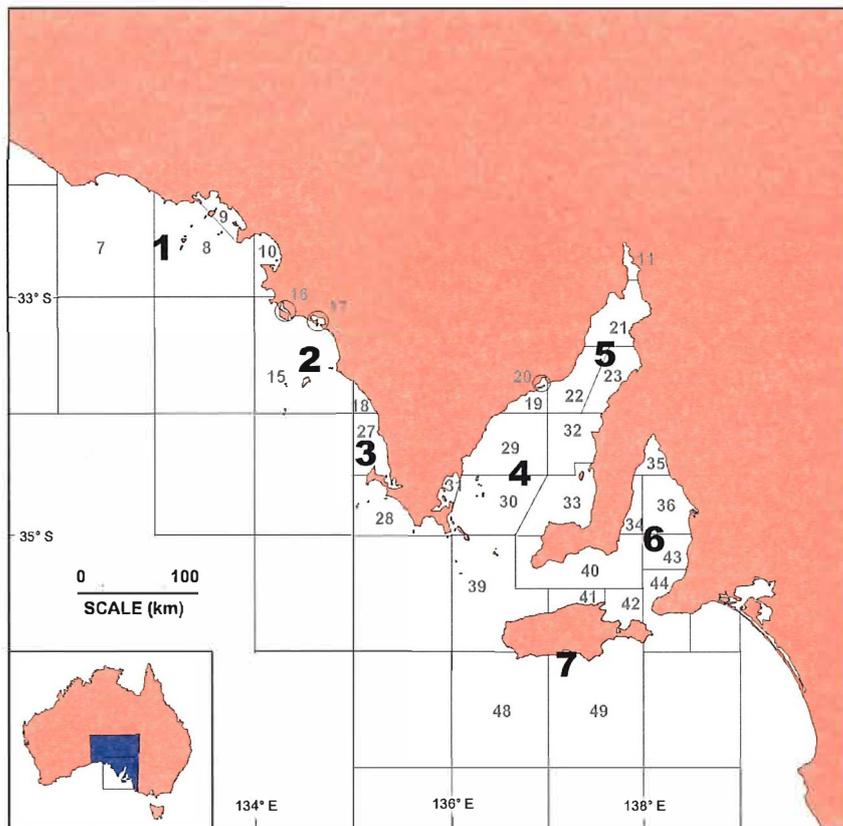


Fig. 8.1 Map of the main fishing region of South Australia showing the Marine Fishing Areas and the seven larger regions for which both commercial and recreational catch are presented.

8.3 Results

Commercial fishery

The long-term trends in statewide catch and effort (Fig. 8.2) indicate that since 1977 handlines have been, and still remain the dominant gear type in the commercial fishery for King George whiting. Through the late 1970's haulnets and gillnets took approximately similar catches, but since the early 1980's the catch of haulnets has increased, whilst that of gillnets has decreased, resulting in the former becoming the second most important gear type. Although catches have been variable over the years, there is a noticeable trend of decreasing catch from the use of handlines and haulnets between 1992 and 1997.

Statewide totals

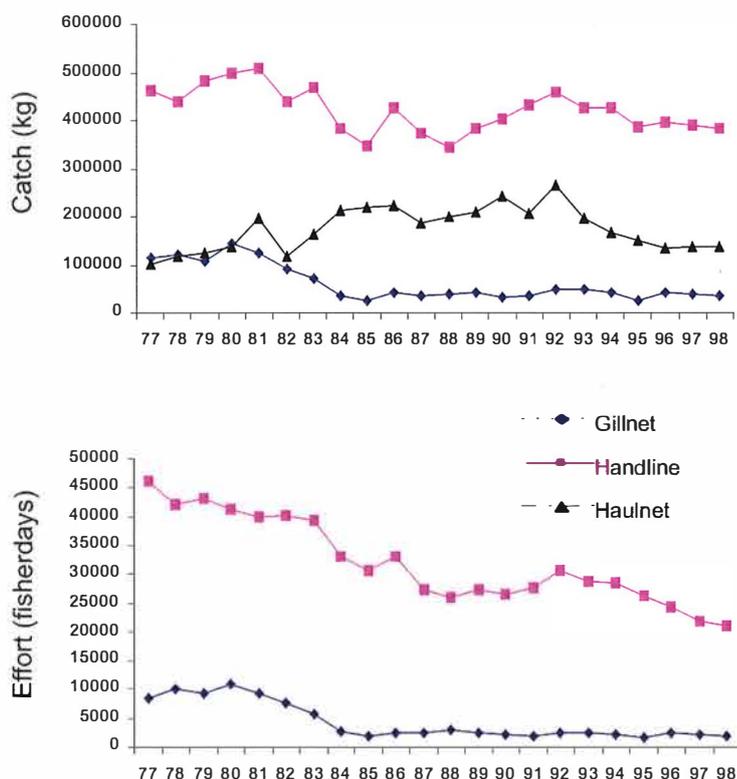


Fig. 8.2 Historical trends in statewide totals for total catch and effort by the commercial fishing sector by gear type.

There has been a substantial reduction in handline effort over the 20 years. For gillnets most effort reduction occurred through the early 1980's. It is problematic to obtain an estimate of total fishing effort in the haulnet fishery because of the difficulties caused by how the targeted and untargeted catch and effort are reported. Consequently, total haulnet effort is not reported on Fig. 8.2, but qualitative assessment of the regional graphs presented below (Figs. 8.3 – 8.10) do suggest a reduction in effort in the haulnet sector over the years.

The substantial reduction in fisherdays in the handline fishery does not accommodate that fishing effort was not standardised to account for technological advances in searching and catching efficiencies. Consequently, the decrease in “effective effort” will not be as dramatic as is suggested in Fig. 8.2.

Far West Coast (Denial and Streaky Bays)

Historically the catch in this region has been dominated by the handline fishery, which on an annual basis is usually the highest of any region across the state (Fig. 8.3). The total catch was highest from 1980-1983, has subsequently decreased and varied around the long term mean and decreased since 1992. Fishing effort was particularly high from 1977 to 1983, but has gradually declined since. CPUE in the handline sector has increased gradually since 1977, with a notable peak from 1989 to 1992. CPUE decreased slightly from 1993 - 1995, but has subsequently increased to the highest recorded levels. The peak of 21.2 kg fisherday⁻¹ was attained in 1997 and dropped noticeably in 1998. Because of the netting ban in this region, the netting sector has made only a relatively small contribution to catch and effort.

Mid West Coast (Baird and Venus Bays)

Handlines, hauling nets and gillnets have each contributed to the catch in these west coast bays, with handlines remaining the dominant methodology (Fig. 8.4). With catches being highly variable from year to year, there is no apparent increasing or decreasing long-term trend for any gear type. Alternatively, the effort for handlines demonstrates a long-term decrease. Effort in the gillnet sector has been steadier than for handlines. Despite significant inter-annual variability there appears to be an increasing trend in CPUE of the handline sector. There is no such trend apparent for gillnets.

Haulnet catch on the Mid West Coast is less than that of handlines and gillnets, and although variable, suggests a substantial decrease since 1992 (Fig. 8.4). Targeted haulnet effort has decreased over the years, however, effort directed at other species, resulting in by-catch of

King George whiting, has increased since 1991. Since catch by haulnets is quite low, trends in CPUE are very variable and unlikely to effectively reflect stock biomass.

Coffin Bay

Up to 1988 handlines and nets contributed substantially to the catch from Coffin Bay (Fig. 8.5). After this the catches diverged, that from haulnets increased, and that from lines decreased until 1994, after which the haulnet catch decreased to zero, and the handline catch increased, but has subsequently declined. Such variation reflects trends in effort. The haulnet effort has been reduced to zero due to the netting closure imposed in 1995. Handline effort decreased substantially until 1993, increased, and then subsequently decreased since 1995. Gillnet catch and effort have always been low in Coffin Bay, and both have decreased since 1993 eventually to zero in 1997. CPUE of the handline and gillnet sectors increased substantially until 1995. Although there was a sharp decline in handline CPUE in 1996, the CPUE in 1997 and 1998 remain well above the long-term average.

Effort in the haulnet sector was generally high but variable for a long period until 1994, after which there was a significant decrease, relating to the netting closures introduced in 1995. CPUE of the haulnet sector, although variable through the years, does not reflect a consistent increase or decrease, except for the decline to zero between 1995 and 1997.

Southern Spencer Gulf

Handlines are the most significant gear type in this region, followed by haulnets and gillnets (Fig. 8.6). Catch in the handline sector has been highly variable through the year, but shows no long-term trend despite that there has been substantial reduction in effort. Gillnet catches dropped off around 1983 because of a reduction in effort. CPUE for both handlines and gillnets have increased substantially over the years.

The catch of the haulnet sector increased between 1980 – '84, remained steady until 1992 and has subsequently declined. There has been a reduction in targeted effort which accounts for the decline in targeted catch. However, effort directed at no specific target has remained steady as has the catch. CPUE has remained reasonably consistent from year to year.

Northern Spencer Gulf

Haulnets have been the dominant gear type. Handline catches have declined marginally since

the early 1980's, associated with a substantial reduction in effort (Fig. 8.7). The low catch of the gillnet sector reflects the reduction in effort that occurred between 1980 – '84, and also in 1989, when it was reduced to virtually zero. CPUE of the handline sector has increased relatively steadily over the two decades, whilst that of the gillnet sector has been highly variable, due to the minimal effort in this sector.

Haulnets have historically provided the highest catches in this region, although with significant inter-annual variability. Both targeted effort and non-targeted effort appear to have decreased substantially over time. CPUE has been variable, but does not demonstrate a substantial long-term trend.

Gulf St. Vincent

The handline and haulnet fisheries have contributed approximately evenly to total catch over the years, whilst the gillnet fishery has usually also made a significant contribution to total catch (Fig. 8.8). Targeted effort in both the handline and gillnet sectors have decreased substantially, particularly since 1982. Although the handline CPUE has increased consistently in both sectors since 1977, it still remains the lowest of all of the seven regions.

Targeted catch of the haulnet sector has decreased, reflecting a decrease in targeted effort. However, the non-targeted catch and effort have increased. The targeted and non-targeted CPUE have increased since 1977.

Kangaroo Island

Handlines and hauling nets have been the main gear types in this region (Fig. 8.9). Handline total catch decreased from 1977 to 1986, then increased consistently due to changes in effort. Effort in the gillnet sector has decreased substantially since 1983 and is now insubstantial. CPUE of the handline sector has been increasing constantly since 1977.

The hauling net catch has increased consistently over the two decades. The catch and effort data, reflect a significant change from targeted to untargeted catch and effort between 1991 and 1992. This more likely reflects the way that such data are reported by fishers than a change in fishing methodology. This, therefore, makes it difficult to interpret catch, effort and CPUE data for the hauling net sector.

Far West Coast

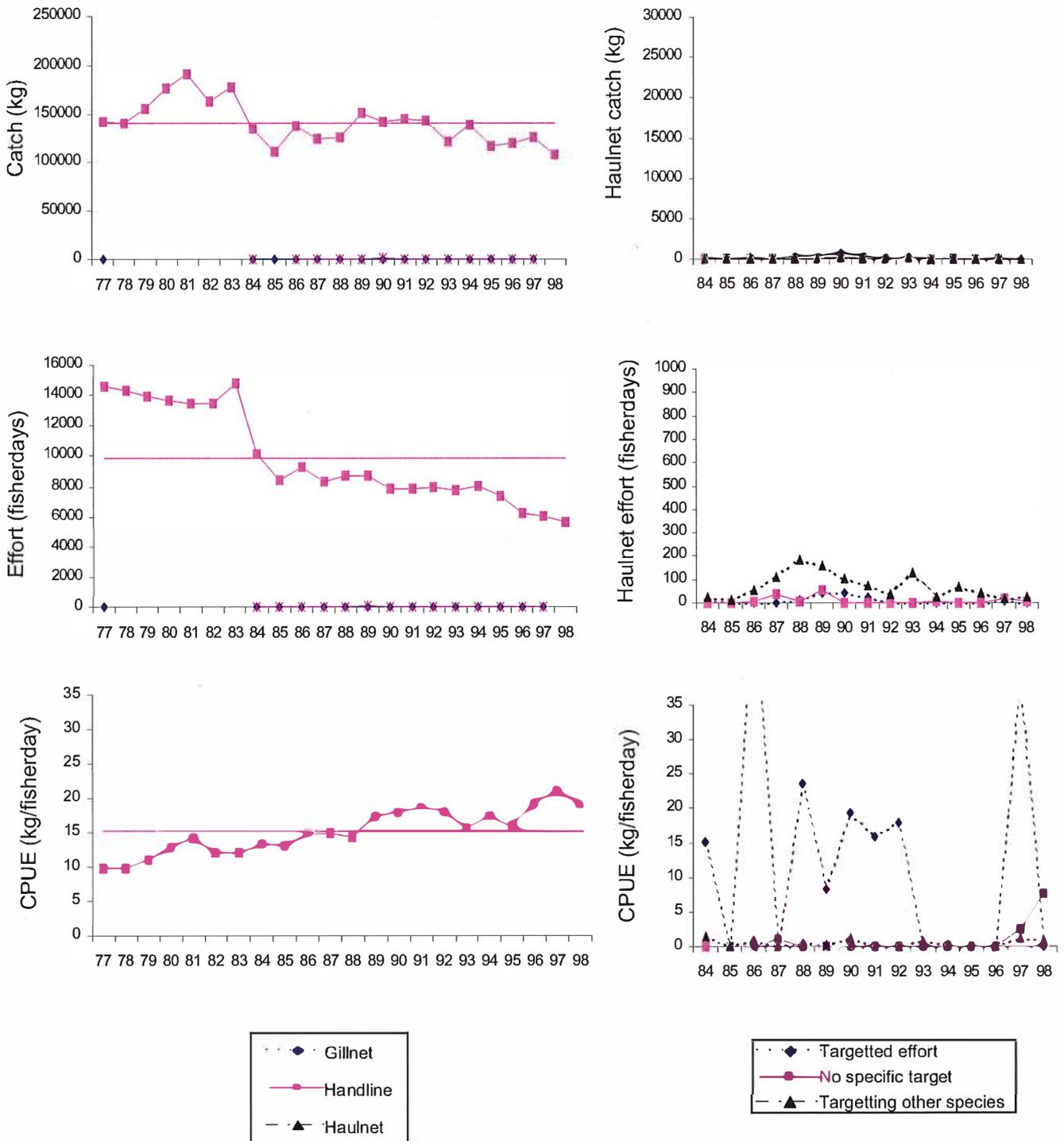


Fig. 8.3 Far West Coast. Left hand graphs show the total catch for each gear type, and effort and CPUE for handlines and gillnets. Right hand graphs relate to haulnets, showing catch, effort and CPUE for the three effort categories. Horizontal lines represent long-term means.

Mid West Coast

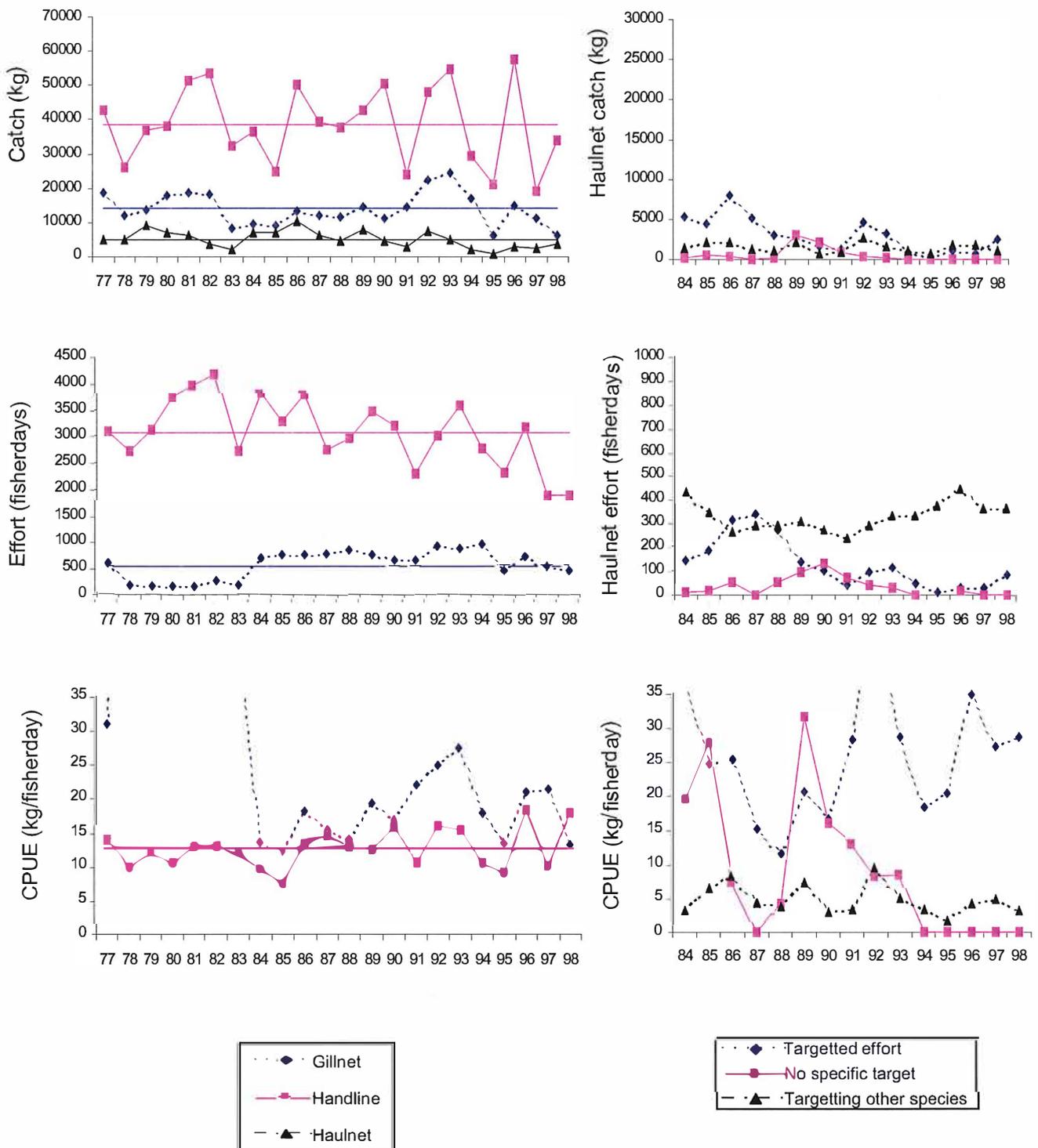


Fig. 8.4 Mid West Coast. Left hand graphs show the total catch for each gear type, and effort and CPUE for handlines and gillnets. Right hand graphs relate to haulnets, showing catch, effort and CPUE for the three effort categories. Horizontal lines represent long-term means.

Coffin Bay

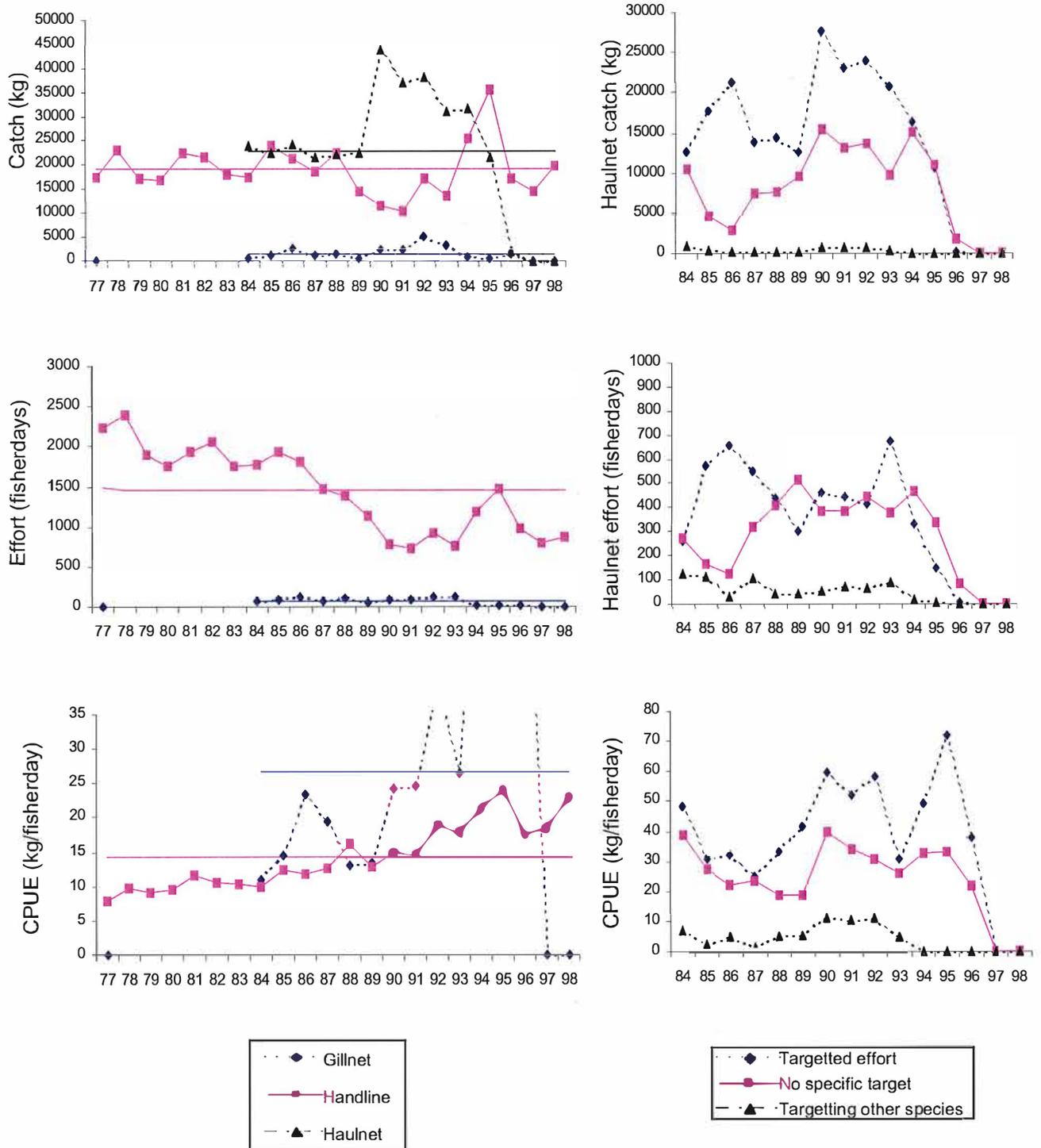


Fig. 8.5 Coffin Bay. Left hand graphs show the total catch for each gear type, and effort and CPUE for handlines and gillnets. Right hand graphs relate to haulnets, showing catch, effort and CPUE for the three effort categories. Horizontal lines represent long-term means.

Southern Spencer Gulf

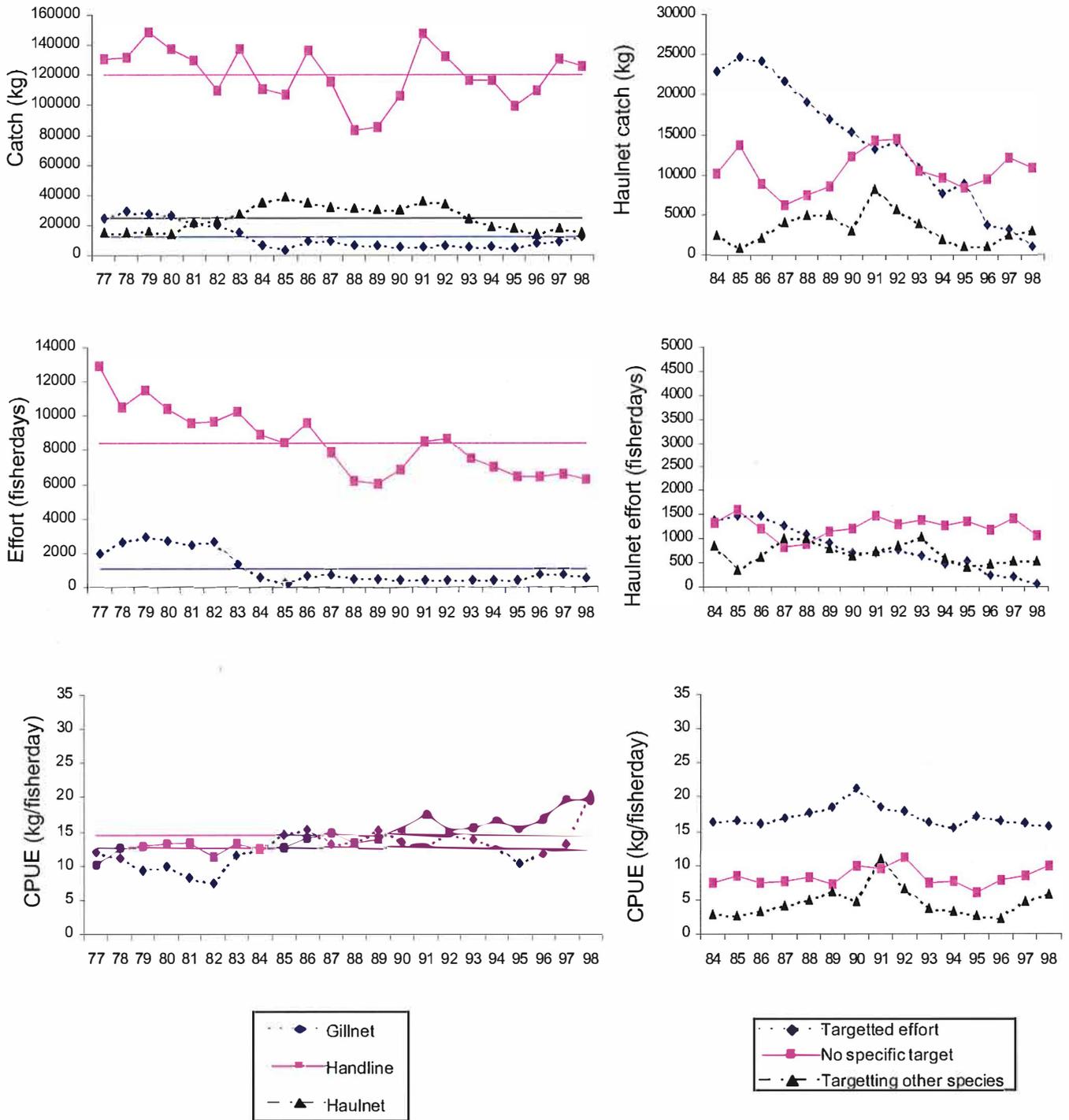


Fig. 8.6 Southern Spencer Gulf. Left hand graphs show the total catch for each gear type, and effort and CPUE for handlines and gillnets. Right hand graphs relate to haulnets, showing catch, effort and CPUE for the three effort categories. Horizontal lines represent long-term means.

Northern Spencer Gulf

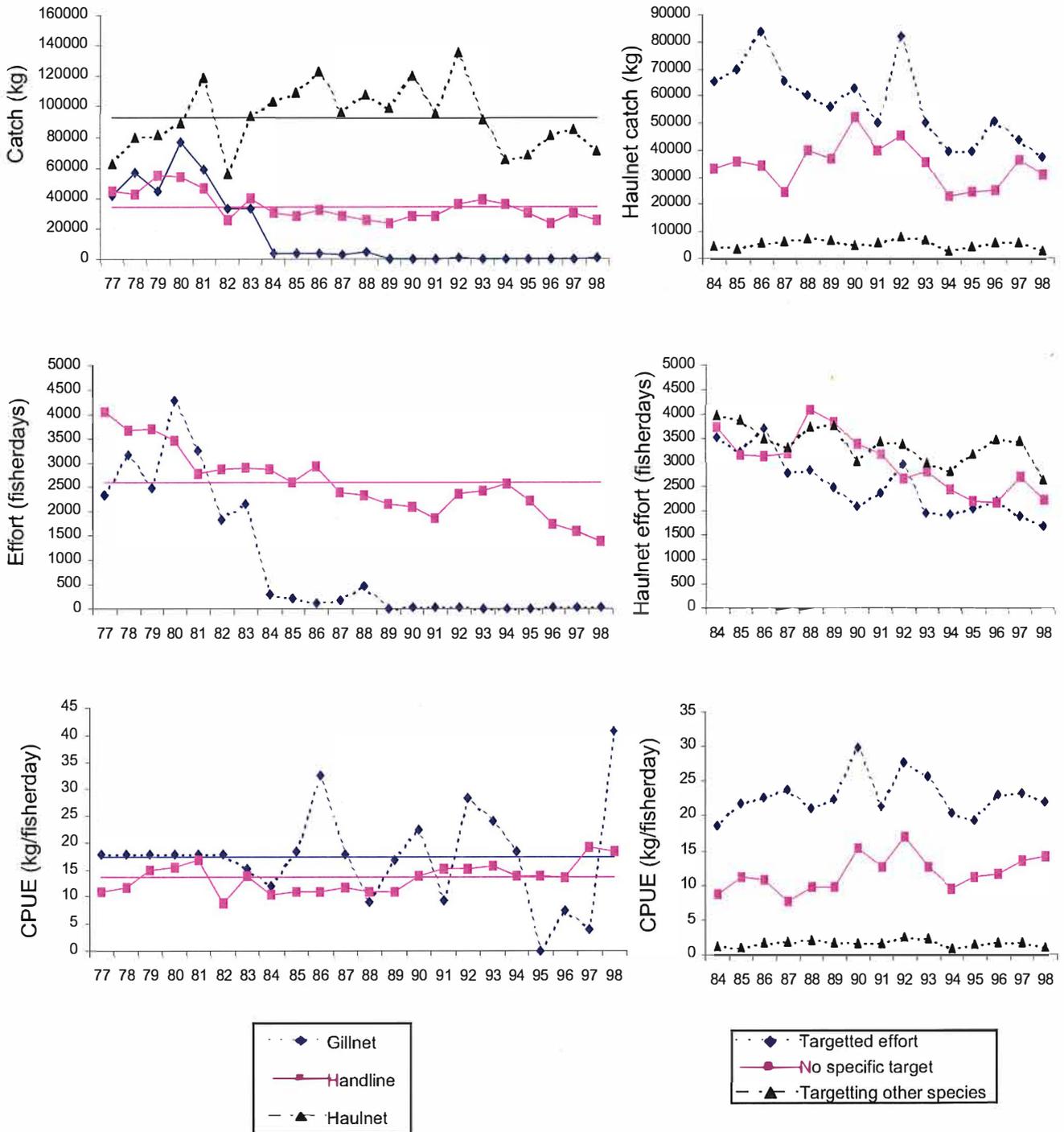


Fig. 8.7 Northern Spencer Gulf. Left hand graphs show the total catch for each gear type, and effort and CPUE for handlines and gillnets. Right hand graphs relate to haulnets, showing catch, effort and CPUE for the three effort categories. Horizontal lines represent long-term means.

Gulf St. Vincent

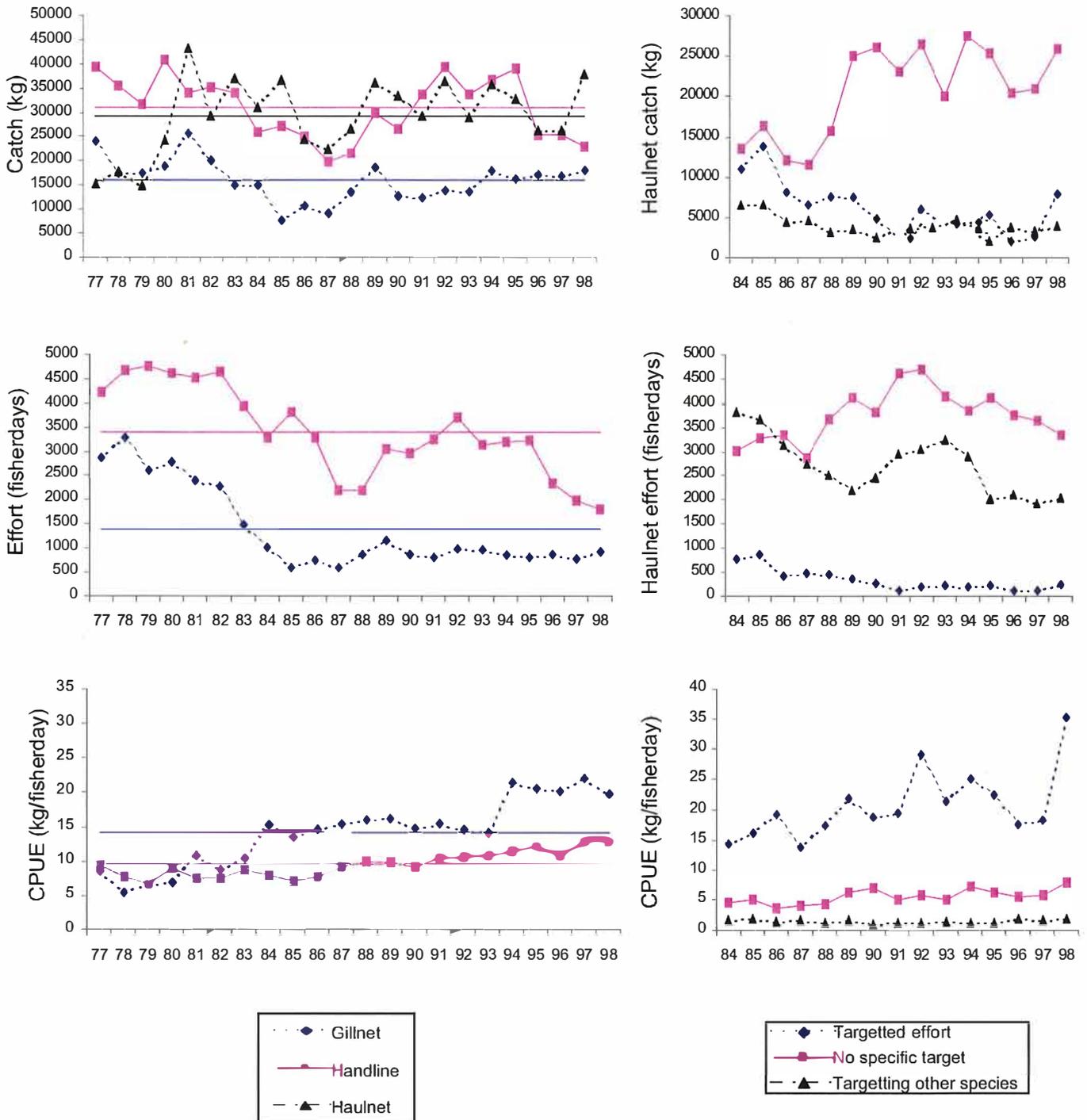


Fig. 8.8 Gulf St. Vincent. Left hand graphs show the total catch for each gear type, and effort and CPUE for handlines and gillnets. Right hand graphs relate to haulnets, showing catch, effort and CPUE for the three effort categories. Horizontal lines represent long-term means.

Kangaroo Island

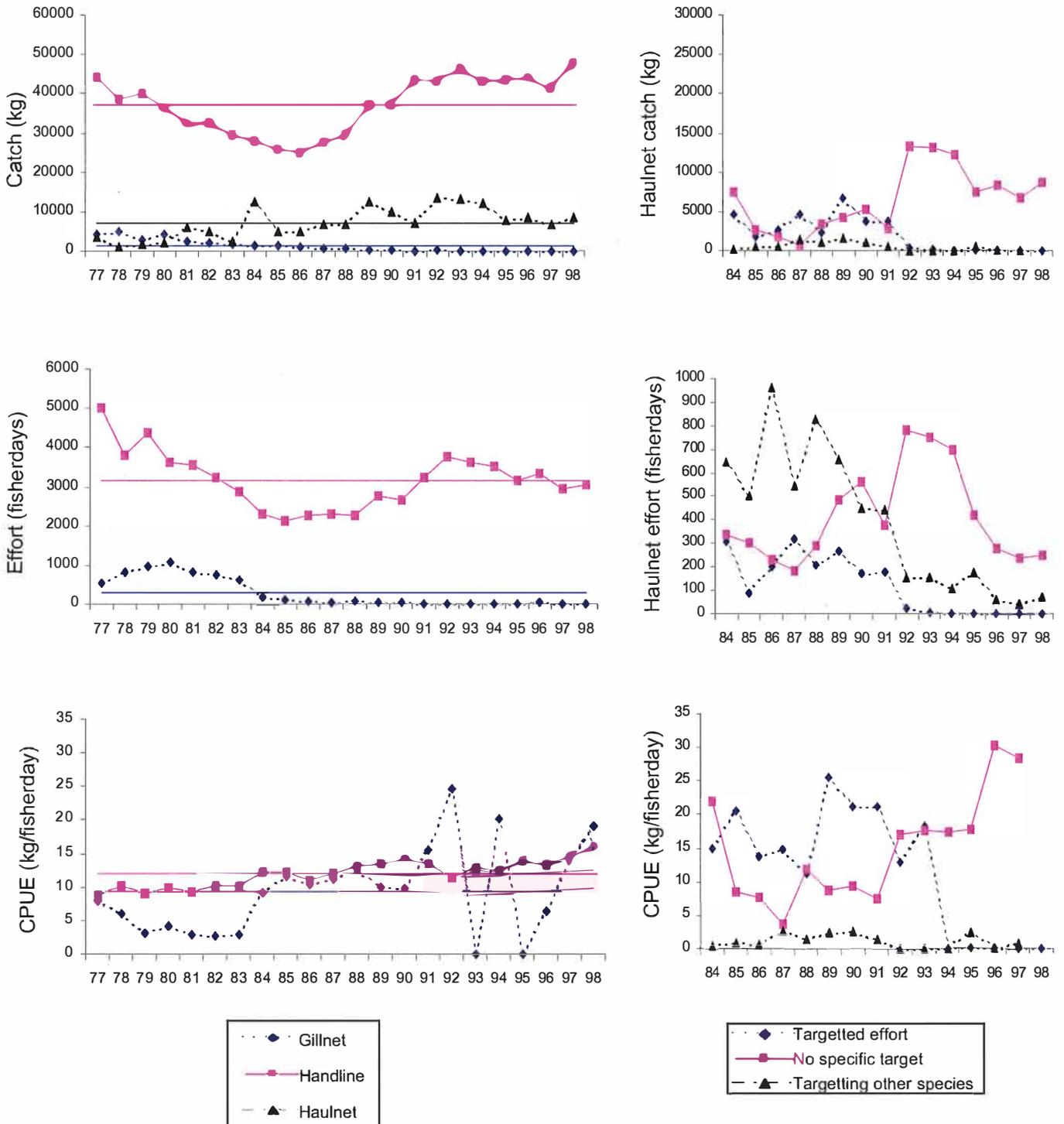


Fig. 8.9 Kangaroo Island. Left hand graphs show the total catch for each gear type, and effort and CPUE for handlines and gillnets. Right hand graphs relate to haulnets, showing catch, effort and CPUE for the three effort categories. Horizontal lines represent long-term means.

Temporal variation in effort and CPUE

It is difficult to discern the overall trends in effort and CPUE because of the need to separate these into gear types, which is even further complicated by having to divide the haulnet effort and CPUE into three different categories. The best datasets with which to assess temporal trends in effort and CPUE are those from the handline sector. These relationships were quantified by linear regression analysis and the slopes of the relationships used as an estimate of the rate of effort reduction, the % reduction in effort, the rate of increase in CPUE and the % increase in CPUE that occurred between 1977 and 1998 in each region (Table 8.2).

Table 8.2 - Results of rate of reduction in linefishing effort, and increase in catch rate for each fishing region for the period of 1977-1998, determined by regression analysis of data presented in Figs. 8.3 – 8.9.

Region	Rate of reduction in effort in effort fisherday. year ⁻¹	Effort in 1997	Effort in 1998	% reduction	Rate of increase in CPUE (kg. fisherday ⁻¹ year ⁻¹)	CPUE in 1977	CPUE in 1998	% increase in CPUE
FWC	441.9	14625	5661	61.3	0.446	9.8	19.1	95.7
MWC	52.3	3091	1888	38.9	0.149	13.8	17.9	29.7
CB	71.1	2231	865	61.2	0.666	7.8	23.0	195.4
SSG	256.0	12913	6287	51.3	0.337	10.1	20.0	96.7
NSG	96.8	4060	1388	65.8	0.198	10.9	18.4	69.5
GSV	115.8	4227	1797	57.5	0.242	9.3	12.9	39.3
KI	33.7	5010	3070	38.7	0.255	8.8	15.6	76.2

On the Far West Coast, the reduction in effort in the handline sector has been substantial, and associated with a significant increase in CPUE (Table 8.2). The Mid West Coast has experienced the lowest rate of reduction in linefishing effort, and there has been only a minimal rate of increase in CPUE. The linefishing effort in Coffin Bay has been reduced by >60% but associated with a huge change to CPUE. This is despite the considerable hauling net effort in this region through the early 1980s and early 1990s.

In Southern Spencer Gulf, linefishing is the dominant gear type, and effort has decreased by 51.3% over the period from 1977 to 1998 (Table 8.2). This has been associated with a 96.7% increase in CPUE. In Northern Spencer Gulf, where hauling nets dominate the catch and effort, there has been a 65.8% reduction in fishing effort, resulting in a 69.5% increase in CPUE.

In Gulf St. Vincent, handline effort has decreased substantially, and is associated with a consistent but slow increase in CPUE over the 20 year period (Table 8.2). Nevertheless, the initial catch rates here were originally low, so the absolute change to catch has not been as substantial as in other regions. This may be due to the significant haulnet and recreational components to catch and effort in this region. At Kangaroo Island, handline effort has decreased marginally, which is associated with a substantial increase in CPUE over the 20 years.

Recreational Fishery

Spatial comparison

Over the period of the recreational boat survey, 631 sample-days were surveyed during which 3,513 interviews were conducted (McGlennon and Kinloch 1997). Total annual recreational boat fishing effort was estimated at 988,980 boat hours, distributed over 200,000 boat trips, of which 40.6% were targeting King George whiting. The total catch of all major species was 3,770,256 fish, of which 1,154,662 (30.6% of total) were King George whiting.

Table 8.3 - Summary of results of catch and targeted effort on King George whiting by the recreational boat fishing sector in South Australia, based on the survey of the recreational boat fishery between 1995 and 1996 (McGlennon and Kinloch 1997).

Region	Total catch (kgs)	Total catch (numbers)	Targeted effort (boatdays)	CPUE (kg/boatday)	CPUE (no/boatday)
FWC	21,100	94,039	4,537.1	4.65	20.7
MWC	5,800	35,466	3,871.3	1.50	9.2
CB	21,300	110,184	7,039.4	3.03	15.7
SSG	80,500	274,220	15,605.8	5.16	17.6
NSG	51,900	227,269	12,267.7	4.23	18.5
GSV	85,100	399,536	33,230.9	2.56	12.0
Total	265,700	1,140,714	76,552.2		

Of the estimated catch of King George whiting, 98.8% was taken in Regions 1 – 6 of the fishery regions for which commercial fishery data were presented above (Table 8.3).

Targeted recreational effort decreased from east to west, probably reflecting trends in human population density, with Gulf St. Vincent having the highest recreational effort due to the influence of metropolitan Adelaide. Total catches also decreased from east to west, but CPUE was variable amongst the regions. The two Spencer Gulf regions and the Far West Coast gave the highest estimates of recreational catch, whilst Gulf St. Vincent and the Mid West Coast produced the lowest.

8.4 Discussion

Comparison of commercial and recreational fisheries

Both the commercial and recreational sectors contribute substantially to the King George whiting fishery. In the period from April 1995 - March 1996 the estimated total catch was 783.6 tonnes which represented >3,000,000 individual fish. Of this total catch by weight, approximately one third was taken by the recreational sector and two thirds by the commercial (Table 8.4). The relative catch of the two sectors varied amongst regions. The proportion taken by recreational fishers decreased with increasing distance from metropolitan Adelaide.

Total fishing effort directed at King George whiting was 250,000 boat days over the 12 month period (Table 8.5). The relative proportions contributed by recreational and commercial fishers also varied regionally. The level of recreational fishing effort and its relative contribution to the total was least on the Far West and Mid West Coasts. Recreational effort and its relative proportion increased in Spencer Gulf. However, both these parameters attained their maximum in Gulf St. Vincent. The substantial recreational fishing effort in Gulf St. Vincent presumably reflects the proximity to metropolitan Adelaide, which is the main population centre in the state.

Table 8.4 - Comparison of total catches of King George whiting between the recreational boat and commercial sectors for six fishery regions through the period of April 1995 to March 1996 (McGlennon and Kinloch 1997).

Region	Recreational Catch (tonnes)	Commercial Catch (tonnes)	Total Catch (tonnes)	% of total by rec fishery
FWC	21.1	112.6	133.7	15.8
MWC	5.8	33.2	39.0	14.9
CB	21.3	54.5	75.8	28.1
SSG	80.5	124.5	205.0	39.3
NSG	51.9	96.7	148.6	34.9
GSV	85.1	90.7	175.8	48.4

Table 8.5 - Comparison of total fishing effort on King George whiting between the recreational boat and commercial sectors for the six main fishery regions (McGlennon and Kinloch 1997).

Region	Recreational Effort (boatdays)	Commercial Effort (boatdays)	Total Effort (boatdays)	% of total by rec fishery
FWC	8203	7355	15558	52.7
MWC	5811	3115	8926	65.1
CB	10302	2431	12733	80.9
SSG	36480	11043	47523	76.8
NSG	36318	11140	47458	76.5
GSV	93079	13521	106600	87.3

Commercial fishery

According to the best information available the commercial sector is responsible for the majority of the catch of King George whiting in South Australia (McGlennon and Kinloch 1997). Although fishers in this sector use a variety of gear types the dominant ones used to target this species are handlines, hauling nets and gill nets, in order of decreasing significance. In general, total catches have been quite consistent, but since 1992 have presented a slow but consistent decline. In the past 4 years the value of the commercial catch decreased from \$5,597,000 in 1994/95 to \$3,686,000 in 1997/98 (Knight and Tsolos 1999). There was a consistent decrease in the handline fishing effort between 1977 and 1998, which is particularly evident for the period of 1992 to 1998. Discerning long term trends in effort in the haulnet sector is not easy because of the different target categories. Nevertheless qualitative assessment of the data in Figs. 8.3 - 8.9 suggests some decrease in haulnet effort at both the Mid west coast, northern Spencer Gulf as well as the obvious decline in Coffin Bay that was associated with the netting closure. At Kangaroo Island there has been some decline in haulnet effort from 1992 to 1998, but in both southern Spencer Gulf and Gulf St. Vincent haulnet effort has remained relatively consistent.

It appears, therefore, that decreasing regional catches are a reflection of decreasing effort particularly of line fishers, but also some haulnet effort. Temporal trends in effort reflect the reduction in the number of fisherdays, but do not accommodate any recent advances in searching or fishing technology. Consequently, the change in "effective" fishing effort is unlikely to have been as dramatic as the decrease in number of fisherdays. The general trend in CPUE has been one of increase in most regions and in 1997 and 1998 attained the highest levels yet recorded. This may reflect that the decrease in fishing effort has meant less pressure on fish stocks, and resulted in higher catch rates. However, this may also involve a component of increase in "effective" effort, where even though there are fewer fisherdays, the searching and catching ability of the fishers has improved over the years.

8.5 References

Knight MA, Tsolos A (1999). South Australian Fisheries and Aquaculture Information and Statistics Report. SARDI Research Report Series.

McGlennon D and Kinloch MA (1997). Resource allocation in the South Australian marine scalefish fishery. FRDC project 93/249, Final Report.

CHAPTER 9. SEASONAL GROWTH FROM LENGTH-AT-AGE SAMPLES

R. McGarvey

9.1 Introduction

Yearly seasonal variation in fish growth has been measured by a range of methods including mark-recapture (Francis et al. 1992; Coggan 1997) and otolith annulus diameter increments in combination with tetracycline marking (Panfili et al. 1994; Fabré and St. Paul 1998). For estimating growth of commercial fish species, lengths-at-age, obtained as counts of yearly otolith annuli from samples of the harvest, are most commonly employed. We present a model for estimating parameters of seasonal growth by fitting to length-at-age samples of King George whiting from South Australia (Fig. 9.1).

The model applies to temperate fish species, assuming yearly spawned (or periodic) cohorts and seasonal (or periodic) variation in growth rate. It assumes a von Bertalanffy formula for mean length versus age generalised by an added exponent parameter. (See Schnute (1981) or Akamine (1993) for a brief summary of various adapted von Bertalanffy models.) The distribution of lengths-at-age was modelled by a normal likelihood with standard deviation assumed to vary linearly with age. The model was applied to estimate continuous formulas for monthly distributions of length-at-age for 6 otolith data sets of South Australian King George whiting. A model employing a similar error structure, standard deviation allowed to vary linearly with the independent variable, was also employed to fit weight versus length for the 6 data sets.

Hyndes et al. (1998) aged samples of this species in southwestern Australia. Southwestern Australian populations grew faster and reached larger maximum lengths than those from South Australia. The growth analysis of Hyndes et al. (1998) did not consider seasonality, which was less evident in their plotted data, or the explicit distribution of lengths-at-age.

Fish smaller than legal minimum length (LML) captured by commercial and recreational fishers must be returned to the sea. Describing the spread of lengths at each monthly age is of value for assessing populations of heavily exploited species such as King George whiting, where depletion of the legal sizes of the cohort is rapid over monthly time scales. In fishery stock assessment models, where only legal-sized lengths of each yearly cohort are subject to exploitation, model accuracy is improved by dividing the cohort into legal and sub-legal length components.

Omitting fish below LML from length and age samples, inevitable when sampling is of the landed catch, creates an overestimation bias of mean length-at-age. However, samples from the commercial

or recreational harvest are generally obtained at lower cost than samples gathered by researchers. A goal of this growth model was to estimate parameters for mean length and standard deviation of length distribution vs age which are unbiased by the cut-off at LML. This bias was obviated by use of a truncated model likelihood assuming zero probability of capture below LML.

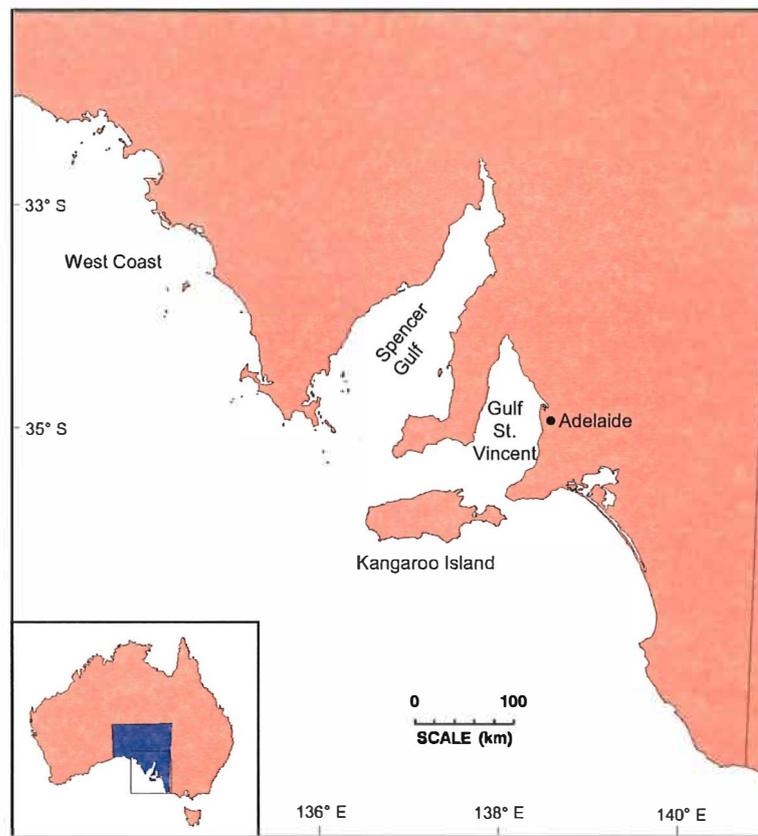


Fig. 9.1 Map of the South Australian coastal waters showing the three regions for which growth analyses are presented in this chapter. The regions are: the eastern region (Gulf St. Vincent, Investigator Strait, Kangaroo Island); Spencer Gulf; the west coast of Eyre Peninsula.

9.2 Methods

A total of 11,164 fish were sampled between 1995-1998 from across the main fishery area of South Australia. Most samples were obtained by sub-sampling the commercial catch at local fish processing plants or by purchasing fish from commercial processors. Some samples were provided as frozen fish frames (fillets removed) by recreational fishers, and the remainder were caught on scientific cruises. Each fish was measured for total (TL) and standard lengths (SL) to the nearest mm, and weighed to 0.1 g. Gonads were removed, sexed and weighed. The sagittae, the largest pair of otoliths were removed from each fish for age determination.

Young samples (two and three year olds) were aged by interpretation of the macrostructure of the whole sagittae. For fish with more complex otoliths, the otolith was snapped in two across the posterior/anterior axis through the centre, exposing the transverse face of both halves. One of these was burnt in a bunsen flame, then examined using a binocular dissecting microscope at x6 – x20 magnification. The surface being examined was smeared with immersion oil. The alternating opaque and translucent zones were counted. The periodicity of formation of this macrostructure in sagittae of King George whiting has been validated and the following algorithm developed for conversion of increment count to age (Fowler and Short 1998): $Age_m = (N \times 12) + m_b + m_c$, where age_m = age in months, N = number of opaque zones, m_b = number of months from universal birth date (i.e. 1st May) to the end of the year, m_c = number of months from the start of year to the month of capture.

Some samples of fish were scaled in the commercial processing plant prior to weighing and measuring for length. Although this process did not affect their lengths, it did result in an appreciable loss of weight. Consequently, for estimation of weight-length relationships we corrected the weights of scaled fish using a linear relationship that was derived by weighing 155 fish before and after scaling. This linear relationship was:

$$(\text{Corrected weight}) = 1.0176 (\text{scaled weight}) + 3.5835 \quad (r^2 = 0.99, p < 0.001, df = 154).$$

Samples were subdivided by sex and spatial region, yielding six data sets (Table 9.1). Movement studies based on tag recoveries over three decades suggest three largely self-sustaining subpopulations: Gulf St. Vincent, Spencer Gulf, and West Coast (Fig. 1). Samples were subdivided into these three spatial regions and by sex, yielding 6 data sets (Table 1).

Table 9.1. Summary of data sets, each fish measured for age, length and weight, in the King George whiting analysis. Fishers' (commercial and recreational) samples were regulated by a 280 mm minimum length before September 1995, 300 mm thereafter.

Area	Area abbreviation	Sex	Beginning date	End date	Sample size		
					Researchers	Fishers 280 LML	Fishers 300 LML
Gulf St. Vincent and northern Kangaroo Island	GSV	male	4-Aug-94	17-Feb-99	293	503	1139
		female	4-Aug-94	17-Feb-99	373	615	1343
Spencer Gulf	SG	male	23-Apr-94	30-Sep-97	267	298	924
		female	23-Apr-94	30-Sep-97	363	441	1300
South Australian West Coast	WC	male	27-Apr-94	18-May-97	167	805	608
		female	27-Apr-94	19-May-97	226	857	642

Growth: Length-at-age

Regulation by legal minimum length (LML) requires commercial and recreational fishers to return fish below that size to the water. A truncated distribution was employed as the likelihood. Truncation implies a zero predicted probability of observing a commercially or recreationally sampled fish less than LML. Small numbers of fish of sublegal length were removed from the 6 data sets.

The LML was increased during the period of sampling, in September 1995, from 280 to 300 mm. Thus the likelihood truncation cut-off was a function of date of capture. For commercial and recreational fishery samples, this yielded two forms of likelihood for each age. Sampling carried out on a smaller scale from a research vessel was not subject to LML cut-off. Thus a third, regular untruncated, likelihood form was used to model research samples.

A normal likelihood was chosen to model the distribution of lengths at each age

$$L = \frac{1}{\sqrt{2\pi} \sigma(a_i)} \exp\left[-\frac{1}{2} \left\{ \frac{l_i - \bar{l}(a_i)}{\sigma(a_i)} \right\}^2\right] \quad (1)$$

where l_i = length of fish sample i , and a_i = age of sample i , obtained from count of its otolith annuli.

Model parameters define variation of the normal likelihood length distribution with age. The mean length-at-age was modelled by a seasonally periodic von Bertalanffy growth formula, generalised by the inclusion of an exponent, r :

$$\bar{l}(a_i) = L_\infty \left\{ 1 - \exp \left[-K \left\langle \frac{a_i - t_0}{12} + \frac{u}{2\pi} \{ \sin(2\pi(a_i - \omega)/12) - \sin(2\pi(t_0 - \omega)/12) \} \right\rangle \right] \right\}^r. \quad (2)$$

The independent variable of age, a_i , was defined in integral units of months, with May, the assumed date of birth at mean time of spawning of South Australian King George whiting, being month 1. Division by 12 in the mean length formula preserves the usual interpretation of K where age is in years.

The seasonality function is sinusoidal. Values of the seasonality amplitude parameter, $u > 1$, would permit fish to decrease in length with age at the minimum time of growth. We therefore constrained $u \leq 1$, assuming no shrinking in length occurs. Using sine, the phase parameter, ω , gives the month of maximum growth, with months 1, 13, 25, etc. being May, the assumed month of birth.

The likelihood standard deviation, σ , was modelled permitting linear variation with age:

$$\sigma(a_i) = s_0 + s_1 a_i. \quad (3a)$$

Higher order than linear polynomials for $\sigma(a_i)$ were tried but these, once fitted, did not differ significantly from the linear form (3).

In application to length and age-based fishery modelling, the above formula (3a) for likelihood standard deviation versus age revealed a small inconsistency. In winter months of slowed or nearly zero growth, the purely linear formulation of standard deviation in Equation 3a continues to increase at a constant rate. Assuming instead that the spread of lengths increases in step (proportionally) with increases in mean length, an alternative form for σ , incorporating seasonality of growth, was used:

$$\sigma(a_i) = \frac{s_0}{12} + s_1 \left\{ \frac{u}{2\pi} \{ \sin[2\pi(a_i - w)/12] - \sin[2\pi(t_0 - w)/12] \} + \frac{a_i}{12} \right\}. \quad (3b)$$

The left-truncated normal likelihood, which applies to samples from commercial and recreational fishers,

$$L_i = \begin{cases} \frac{1}{\sigma(a_i)} \exp\left[-\frac{1}{2} \left\{ \frac{l_i - \bar{l}(a_i)}{\sigma(a_i)} \right\}^2\right] & / \left\{ \int_{LML_i}^{+\infty} \frac{1}{\sigma(a_i)} \exp\left[-\frac{1}{2} \left\{ \frac{l - \bar{l}(a_i)}{\sigma(a_i)} \right\}^2\right] dl \right\}, \text{ if } l_i \geq LML_i \\ 0, & \text{ if } l_i < LML_i \end{cases} \quad (4)$$

postulates a probability cut-off of zero for landed samples less than LML and a normal probability, renormalised to 1, for the range of legal lengths. LML is subscripted by the fish sample data point, i , to indicate LML is either 280 or 300 mm depending on fish's date of capture.

Parameters were estimated by minimising the negative sum of log-likelihoods:

$$O = -\sum_{i=1}^n \ln(L_i). \quad (5)$$

Confidence bounds on parameters for each data set were calculated by 1000 bootstrap runs, sampling with replacement from the set of fish samples. For u , constrained by an upper bound, a one-sided standard deviation was used relative to the upper bound estimate ($u = 1$).

Weight-at-Length

Mean (corrected) weight versus total length was modelled by an allometric relationship:

$$\bar{w}(l_i) = \alpha l_i^\beta. \quad (6)$$

A normal likelihood was again chosen. As above, the standard deviation of the likelihood was assumed to vary linearly, in this case, with length:

$$\sigma_w(l_i) = \sigma_{w0} + \sigma_{w1} l_i. \quad (7)$$

Confidence bounds were estimated by a bootstrap of 1000 runs.

9.3 Results

Growth: Length-at-age

The fits for the 3 regions and 2 sexes (Fig. 9.2, 9.3, and 9.4) all yielded strong seasonal periodic trends. Estimates for the seasonality amplitude, u , reached and were constrained at the maximum allowed value of $u = 1$ for 4 of 6 data sets (Table 9.2). The peak month of maximum growth occurred in mid-summer for all 6 data sets, falling later in summer (February) for Gulf St. Vincent.

Table 9.2. Length-age parameters and derived estimates. 95% confidence intervals are 1.96 times the bootstrap standard deviation over 1000 runs given in parentheses as percentages of the estimate value.

parameter	Gulf St. Vincent		Spencer Gulf		West Coast	
	females	males	females	males	females	males
L_{∞}	457.3 (± 1.6%)	408.8 (± 1.4%)	458.6 (± 2.3%)	412.2 (± 1.5%)	428.9 (± 3.5%)	383.7 (± 4.4%)
K	0.59 (± 7.1%)	0.75 (± 10%)	0.70 (± 6.0%)	0.85 (± 5.7%)	0.91 (± 15%)	1.17 (± 18%)
t_0	-7.89 (± 31%)	-12.39 (± 51%)	-21.20 (± 6.9%)	-9.17 (± 0.76%)	-21.23 (± 9.7%)	0.11 (± 960%)
u	1 (± 12%)	0.82 (± 36%)	1 (± 0.27%)	1	1 (± 5.2%)	0.94 (± 29%)
ω	10.17 (Feb) (± 4.4%)	10.74 (Feb) (± 10%)	8.70 (Dec) (± 3.6%)	8.81 (Dec) (± 3.5%)	8.88 (Dec) (± 4.5%)	9.15 (Jan) (± 7.0%)
s_0	290.5 (± 12%)	234.4 (± 10%)	203.6 (± 15%)	271.6 (± 12%)	192.1 (± 26%)	161.0 (± 27%)
s_1	0.86 (± 93%)	1.67 (± 35%)	2.96 (± 26%)	1.01 (± 68%)	3.33 (± 40%)	3.40 (± 36%)
r	2.68 (± 18%)	4.42 (± 45%)	10.85 (± 16%)	6.61 (± 13%)	20.51 (± 27%)	4.22 (± 38%)

Positive values of s_1 were obtained for all data sets, implying a variance of residuals that increased

with age. Lower estimated values of L_{∞} in the West Coast may be an artifact of the absence of sampled fish greater than age 5 (Fig. 9.4).

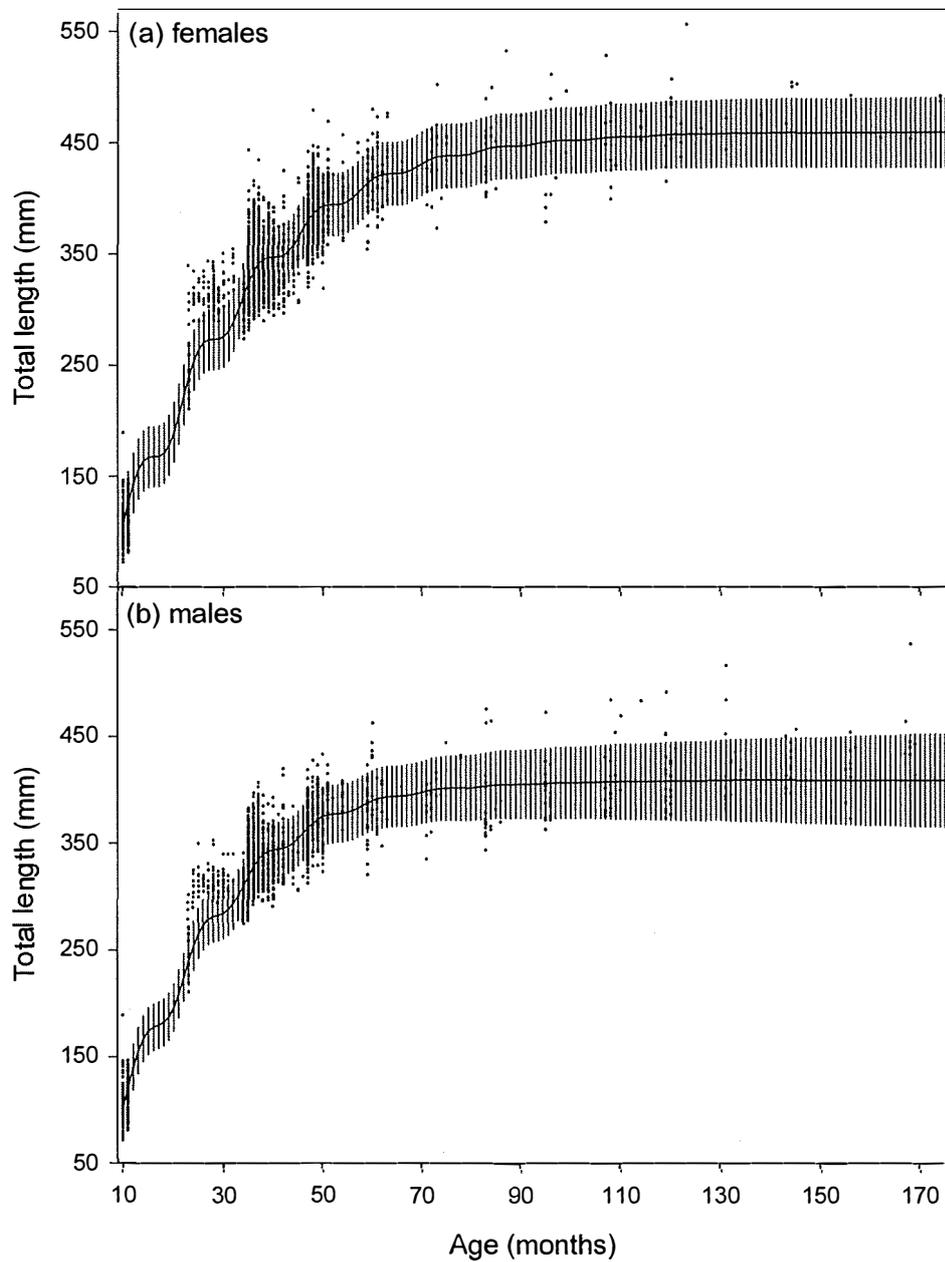


Fig. 9.2. Lengths at age, beginning at 10 months, for Gulf St Vincent samples. Solid line is the generalised seasonal von Bertalanffy mean length with error bars indicating normal likelihood standard deviation. (a) females, (b) males. Dots represent individual observations of length-at-age.

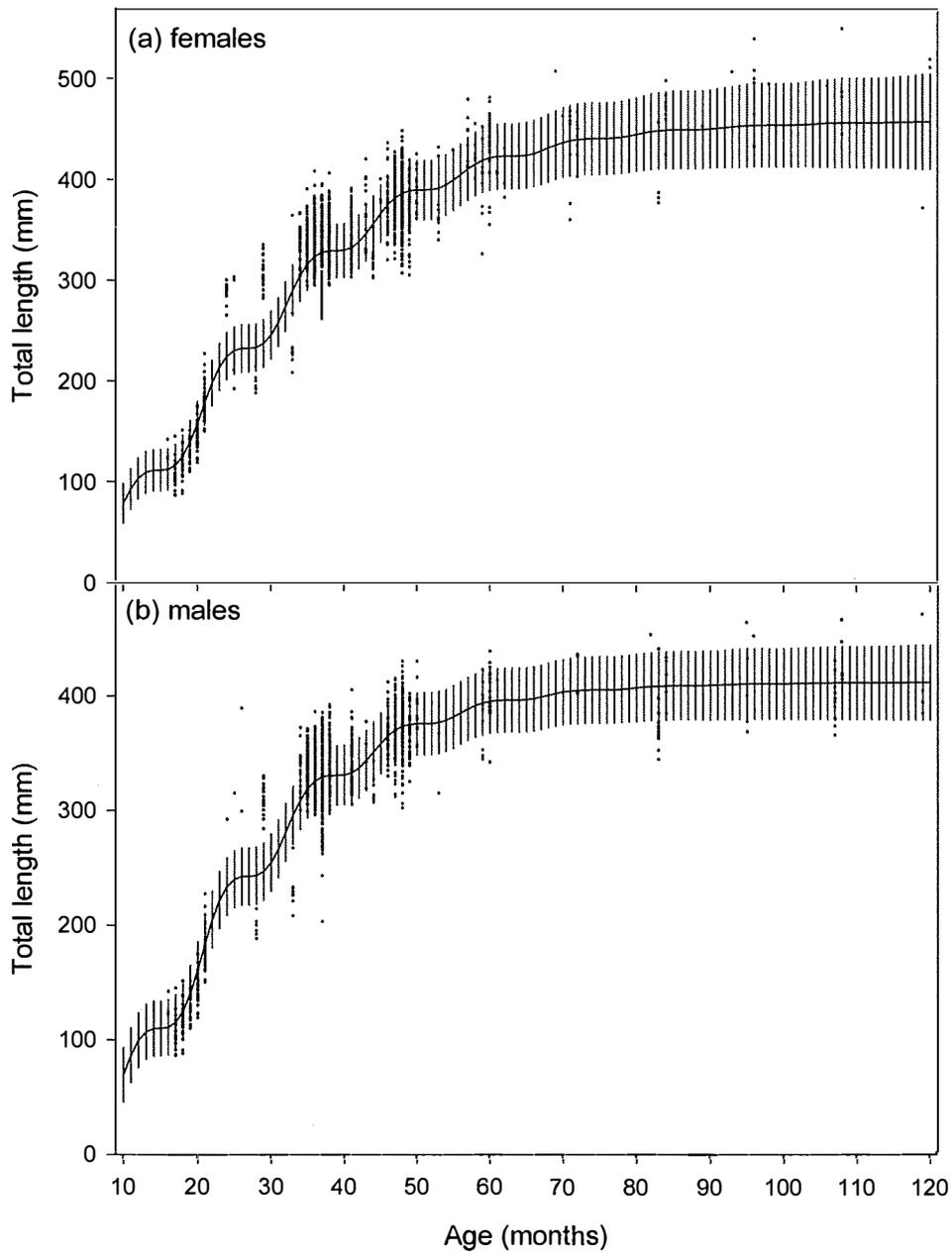


Fig. 9.3. Lengths at age, beginning at 10 months, for Spencer Gulf samples. Solid line is the generalised seasonal von Bertalanffy mean length with error bars indicating normal likelihood standard deviation. (a) females, (b) males.

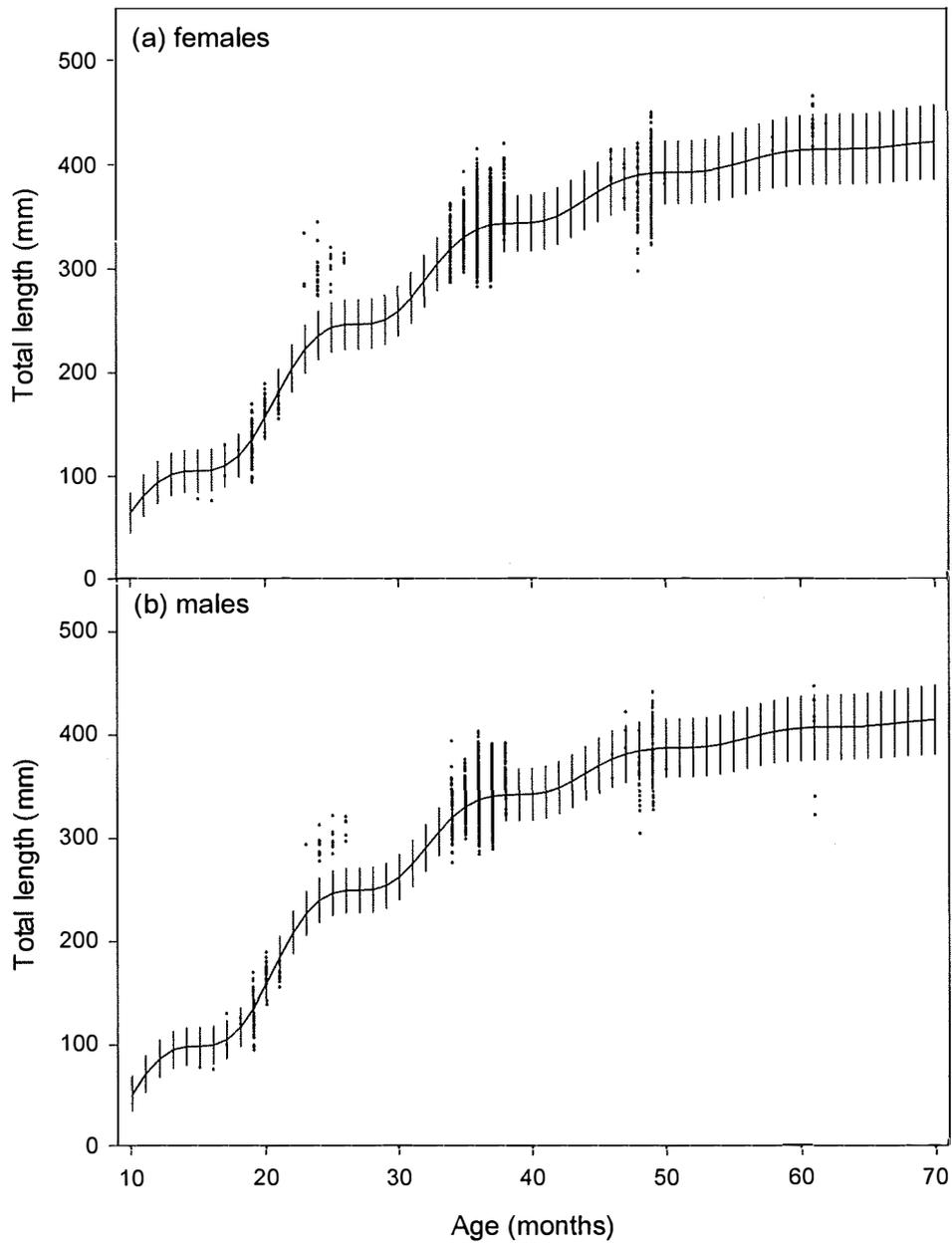


Fig. 9.4. Lengths at age, beginning at 10 months, for West Coast samples. Solid line is the generalised seasonal von Bertalanffy mean length with error bars indicating normal likelihood standard deviation. (a) females, (b) males

The comparison of predicted (estimated maximum likelihood) and observed distributions of lengths-at-age plotted for Gulf St. Vincent females (Fig. 9.5) and males (Fig. 9.6) yielded good fits. Because the estimation likelihood is fitted to formulas for mean (Eq. 2) and standard deviation (Eq. 3) of all ages at once, close fit to the majority of individual length-at-age distributions indicated a mutually consistent growth description among ages and good approximation to the spreads of length at age by the assumed relationships.

The LML cut-off lengths for each normal curve (either 280 or 300 mm) are shown (Fig. 9.5 and 9.6). For younger ages, the truncated shape of the sampled histogram is modelled by the highly non-normal form, effectively the right-hand tail for the youngest length distributions shown (Fig. 9.5 and 9.6, ages 28-36 months). Generally these are also well fitted, suggesting these truncated samples do contribute to the overall growth fit. One exception was the sample of female fish aged 28 months taken under a LML of 280 mm (Fig. 9.5).

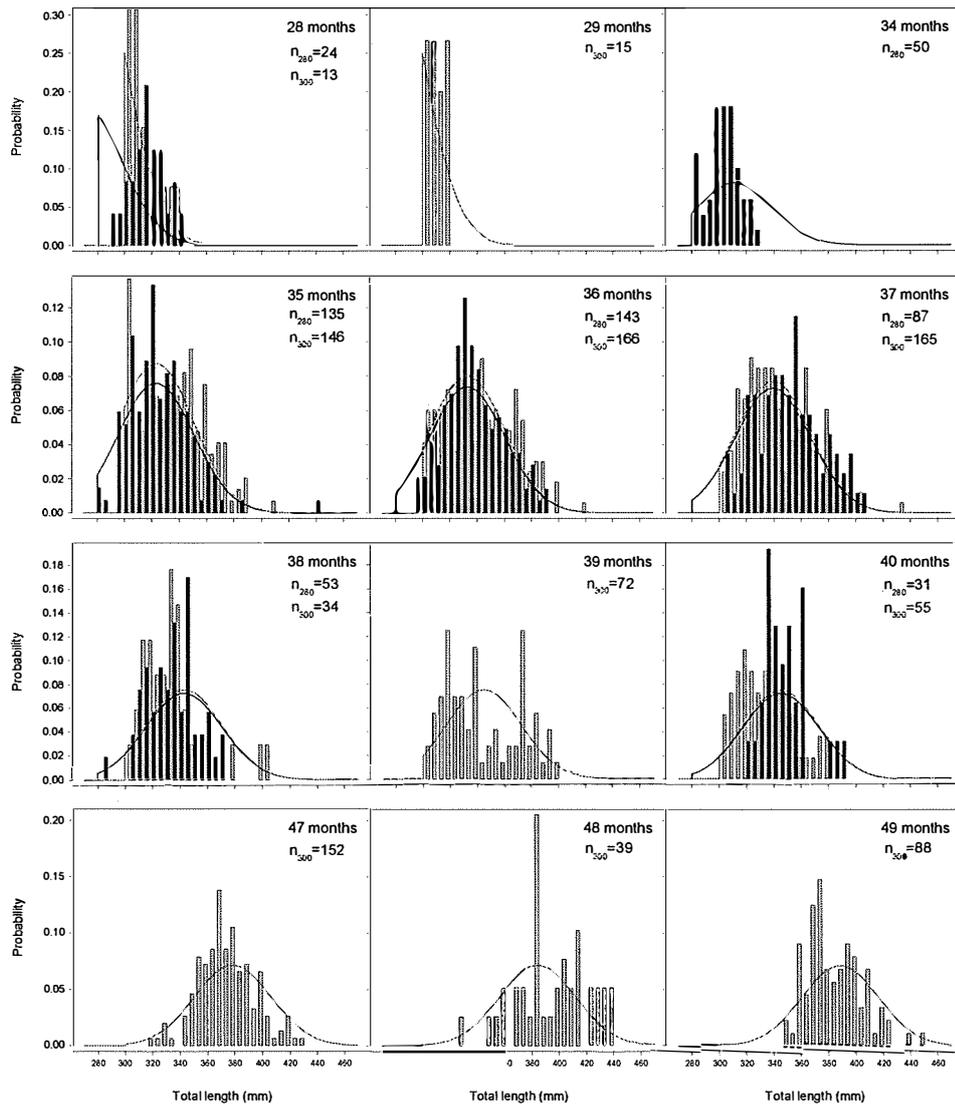


Fig. 9.5. Female Gulf St. Vincent length frequency histograms expressed as proportion of fish caught per 5 mm length class. Ages (by month) illustrated were those of largest sample size. Black bars correspond to fish caught when the fishery was subject to a 280 mm size limit, and grey bars for fish caught under a 300 mm size limit. Normal curves calculated for each size limit have been overlaid for comparison

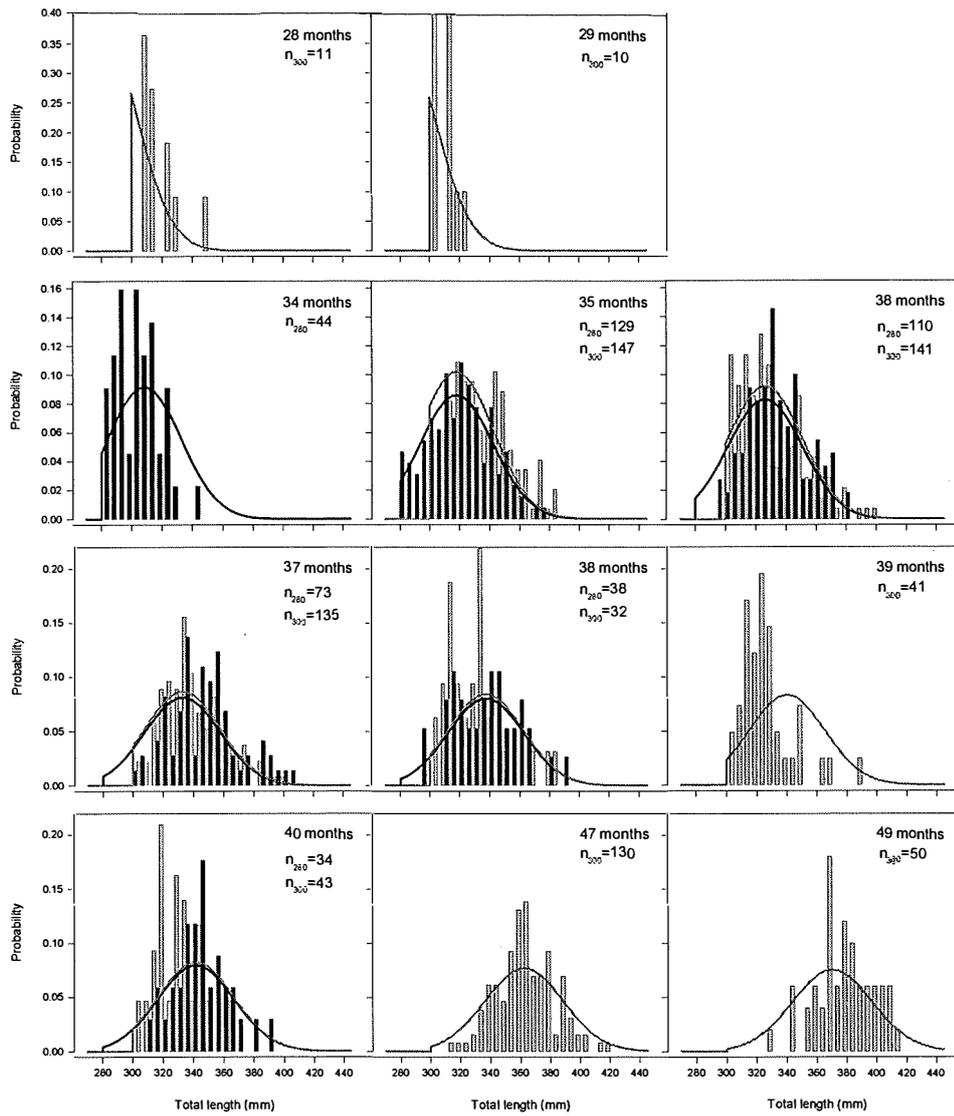


Fig. 9.6. Male Gulf St. Vincent length frequency histograms expressed as proportion of fish caught per 5 mm length class. Black bars correspond to fish caught under a 280 mm size limit, and grey bars for fish caught under a 300 mm size limit.

Weight-at-Length

The fits of sampled weights to length were relatively similar for the 6 data sets (Table 9.3), typified, for example, by Gulf St. Vincent males and females (Fig. 9.7).

Parameters α and β covary strongly. When all four parameters were allowed to freely vary, β differed little from 3.2 for most data sets (Table 9.4). The plotted curves were not visibly altered when β was set to 3.2. Likelihood ratio tests (Kimura 1980; Quinn and Deriso 1999) were therefore carried out to determine whether the model allowing β to vary freely yielded significantly better fits than one with only 3 parameters with β fixed at 3.2.

For all but Spencer Gulf males, β did not differ significantly from 3.2 (Table 9.4). Heavier animals for a given length on average is indicated directly by larger α when β is held fixed. With $\beta = 3.2$ fixed, values of α among the 6 data sets differed little (Table 9.3).

Table 9.3. Weight-length parameters and derived estimates. 95% confidence intervals are 1.96 times the bootstrap standard deviation over 1000 runs given in parentheses as percentages of the estimate value.

parameter	Gulf St. Vincent		Spencer Gulf		West Coast	
	females	males	females	males	females	males
α	1.858x10 ⁻⁶ (± 0.51%)	1.874x10 ⁻⁶ (± 0.63%)	1.880x10 ⁻⁶ (± 0.77%)	1.888x10 ⁻⁶ (± 0.87%)	1.861x10 ⁻⁶ (± 0.40%)	1.887x10 ⁻⁶ (± 0.32%)
β	3.2	3.2	3.2	3.2	3.2	3.2
σ_{w0}	-7.76 (± 15%)	-6.74 (± 12%)	-6.94 (± 13%)	-5.21 (± 24%)	-6.38 (± 13%)	-6.32 (± 6.2%)
σ_{w1}	0.094 (± 8.0%)	0.080 (± 7.2%)	0.087 (± 12%)	0.078 (± 19%)	0.067 (± 8.0%)	0.063 (± 4.6%)

Table 9.4. Likelihood ratio tests comparing differences in the fits between weight-length models which allow β to vary and those which kept $\beta = 3.2$ fixed. Significant difference is indicated by $P < 0.05$.

	Gulf St. Vincent		Spencer Gulf		West Coast	
	females	males	females	males	females	males
β -ESTIMATE (FREE TO VARY)	3.200255	3.200008	3.200031	3.198721	3.200050	3.200021
L-ratio statistic	0.677	0.000	0.005	6.094	0.033	0.006
P-significance (models differ)	0.41	0.99	0.94	0.01	0.86	0.94

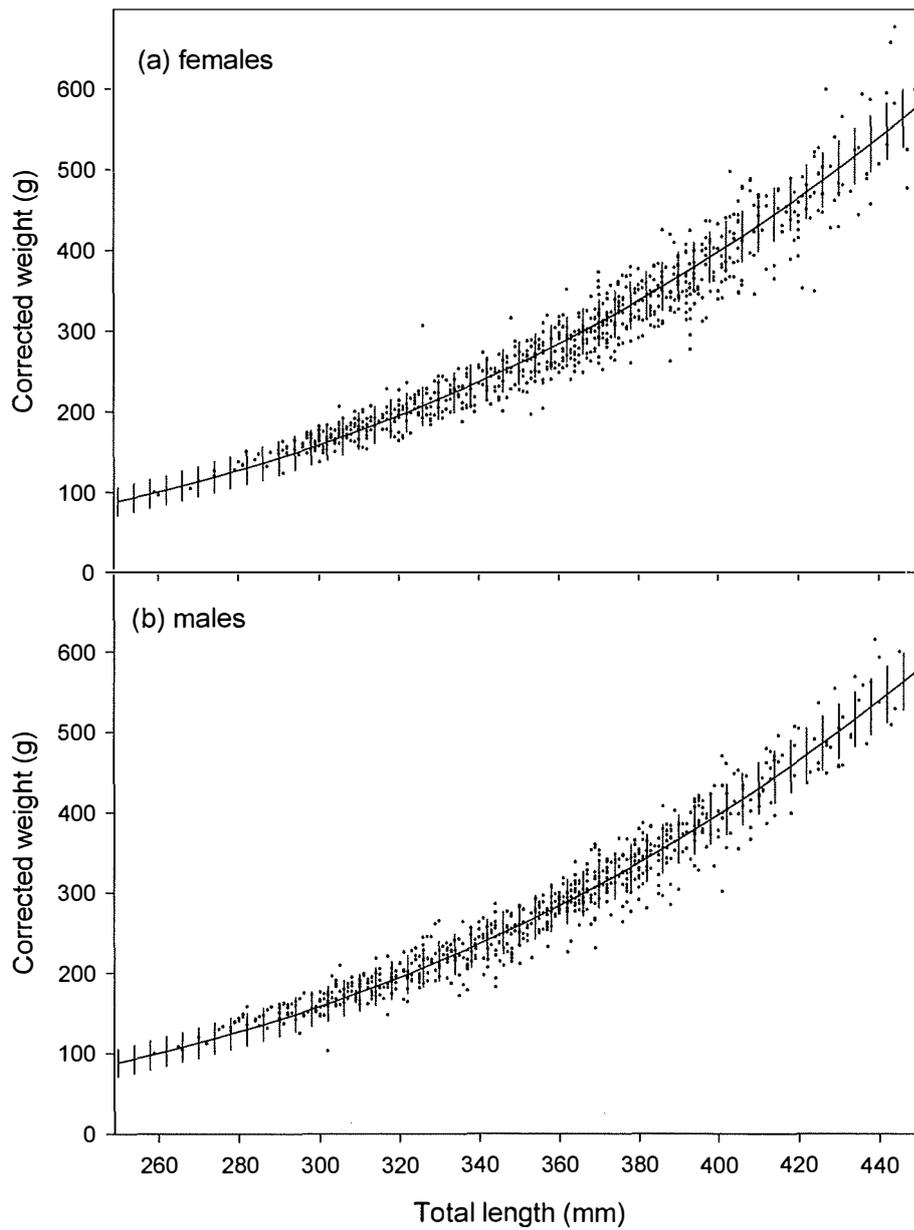


Fig. 9.7. Allometric length vs weight relationship (Eq. 6), fitted to Gulf St Vincent samples. Weights for some fish sample are corrected for the prior removal of scales before weighing. Error bars indicate normal likelihood standard deviation (Eq. 7). (a) females, (b) males.

9.4 Discussion

This model was developed as a compromise between standard non-seasonal von Bertalanffy models fit using a statistical package regression routine in which the distributions of lengths-at-age are not explicit (e.g. Hyndes et al. 1998) and more mathematically complex models (Schnute 1981).

Sinusoidal seasonality (Pauly and Gaschütz 1979) is represented in a now-standard way that preserves the interpretation of t_0 as the age at which length equals zero (Somers 1988; Hoenig and Hanumara 1990). Pawlak and Hanumara (1991) showed that this form of seasonality model yielded statistical advantage. The exponent, r , allowed non-linear variation away from the strict von Bertalanffy form. With these South Australian King George whiting data sets, it improved the model description; fitted r 's ranged from 2 to 20, outside the range describable by the unmodified von Bertalanffy model where $r = 1$ fixed.

Schnute (1981) classified growth models, naming the form we adopted with a single exponent parameter (but without seasonality) the “generalised von Bertalanffy” curve. Other related models include the Richards (1959) model and the more fully general Schnute (1981) model which includes all these as subcases. Akamine (1993) posed theoretical arguments favouring the Richards form, in particular its derivation from a differential equation.

We tried the Richards model with the South Australian King George whiting data sets but found it sometimes failed to converge. Because the Richards form includes both the exponent and its inverse in different places in the formula, it is likely to result in a more numerically challenging minimisation algorithm, in particular, resulting in derivatives with respect to this parameter which are multiply more complex. The two occurrences of the parameter, r , in the Richards formula

$$L = L_{\infty} / \{1 + r e^{-K(t + t_0)}\}^{1/r}$$
, as a factor in front of the negative exponential and as its reciprocal exponent around the entire function apart from L_{∞} , can act in contrary fashion. For $r > 1$, increases in r imply a reduction in length-at-age due to the parameter as reciprocal exponent, and the opposite for the second role the parameter plays in describing mean length. Our experience with the data for King George whiting was that the Richards growth formula was less numerically robust.

Growth was variable, reflected in high standard deviations in lengths-at-age of King George whiting, leaving between a year and two years between the month of crossing into legal size of the first (at ~ 23 months of age) and last 2% of the normal cohort to reach LML. Because fishing mortalities are such that a majority of fish are removed within 12 months of reaching legal size, the explicit representation of the spread of lengths of cohorts as they cross LML allows substantial improvements in stock assessment, notably in fitting only legal sizes to monthly catch totals by weight and sampled

numbers at age. Moreover, the seasonal variations in fishing effort targeted on South Australian King George whiting appear to track the arrival of the bulk of recruits to legal size in autumn and early winter. The growth model presented allowed these features of monthly recruitment to legal size to be captured in the associated population (stock assessment) model with relative ease.

9.5 References

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CHAPTER 10. GROWTH SUBMODEL BY AGE AND LENGTH: MONTHLY ‘SLICES’

R. McGarvey

10.1 Introduction

A new form of age- and length-based formalism for use with monthly fishery population models (‘slice growth’) was developed in this FRDC project. In this chapter we present this method of subdividing the fish population by age and by length in each age. In Chapters 12 and 13 we will discuss the fishery population estimation and simulation model overall, for which this formalism serves as a fundamental component.

South Australian King George whiting are subject to high rates of fishing mortality as new recruits once they grow past legal minimum length (LML). The number in each length subinterval depends on the number of months they have been of harvestable size. In developing a model of the overall fishery in Chapter 12, the two principal data time series to which the population model is fitted are catches-at-age and catch total by weight, both aggregated by monthly time step. Monthly differences in survival rate of fish entering the legal stock and the monthly numbers of newly legal size fish in each cohort will affect both the model-predicted numbers captured in each age group and the predicted catch by weight. For high mortality fisheries such as King George whiting, where monthly data are available, a monthly breakdown by length and age will improve model accuracy.

The age- and length-based method developed in this Chapter serves as the growth submodel. It is based on the fitted normal length-at-age distributions from Chapter 9. The goal was to subdivide the population variable by length as well as age, and to do so in a computationally efficient manner. This was carried out by subdividing each cohort, that is, each age class in the King George whiting model population into length subintervals which we denote as ‘slices’.

10.2 Methods

One option first considered for achieving a growth submodel and population array that made explicit both age and length of each cohort, was to partition the fish in each cohort into fixed uniform length intervals, for instance into 1 mm length bins. Preliminary calculations indicated that this would be computationally unfeasible. To partition the length range of fish in each cohort to cover the highest and lowest 1% by a single bin would require about 100-130 1 mm length bins. More cumbersome

still is the growth description that would be required. With a uniform interval partition of the length axis, a transition matrix would be needed to allocate (i.e. grow) the fish in each length bin to higher bins with each time step. Such a matrix would have $(100-130)^2$ elements (including a likely majority of zeros), and would require corresponding numbers of multiplications and memory and in each time step growth transition. For the King George whiting monthly spatial model, this would render convergence of the objective function unlikely or unwieldy.

An alternative, more computationally efficient partition of the length axis was thus sought. Two sub-goals were posed: (1) a partition of the length distribution so that the newly created length subdivision in each month of age lies exactly on the LML, thus cleanly separating legal and sublegal fish; (2) subdivision of the legal ($>$ LML) fish into length bins that correspond exactly with portions of the cohort entering the fishable stock each month. This would permit a length partition that merged canonically with the discrete monthly time step and fish population array of the estimation and simulation model. In each monthly time step, the number of sublegals in each 'crossing' cohort sliced off as newly legal fish is calculated as a simple proportion of the surviving sublegals. The boundaries of each length slice subinterval are not, therefore, fixed but each 'slice' boundary, would vary with (1) choice of LML, (2) growth parameter set (6, by 3 regions and 2 sexes as in Chapter 9), and (3) monthly age.

King George whiting numbers in each monthly slice are then kept account of in the population model, fishing mortality acting only over the months a length slice is in the legal stock. This slice breakdown (see Figure 10.1) for a cohort is retained while the cohort has components on either side of the LML.

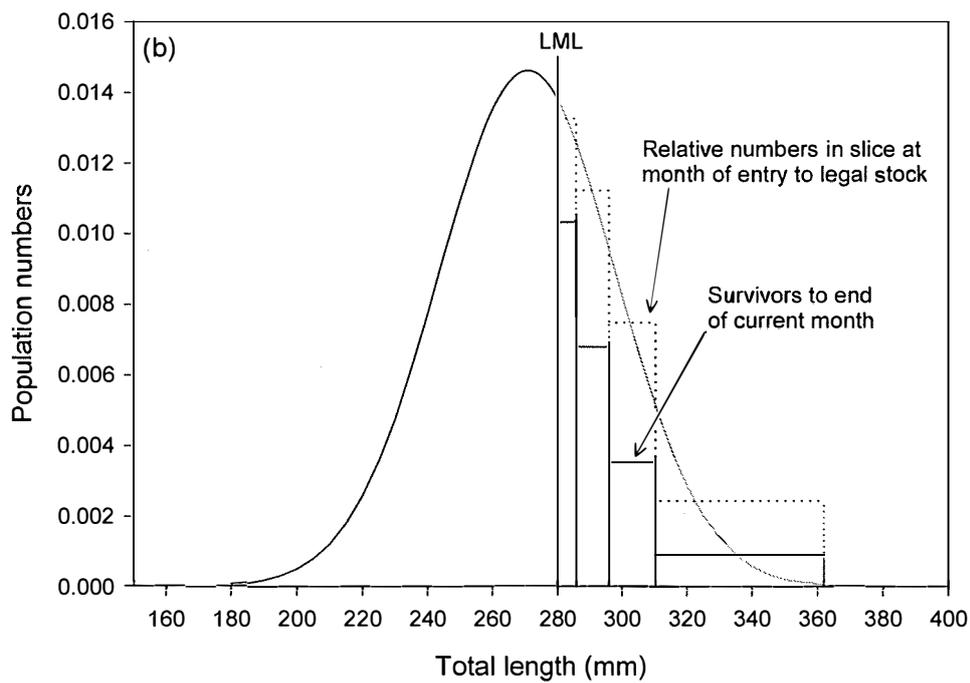
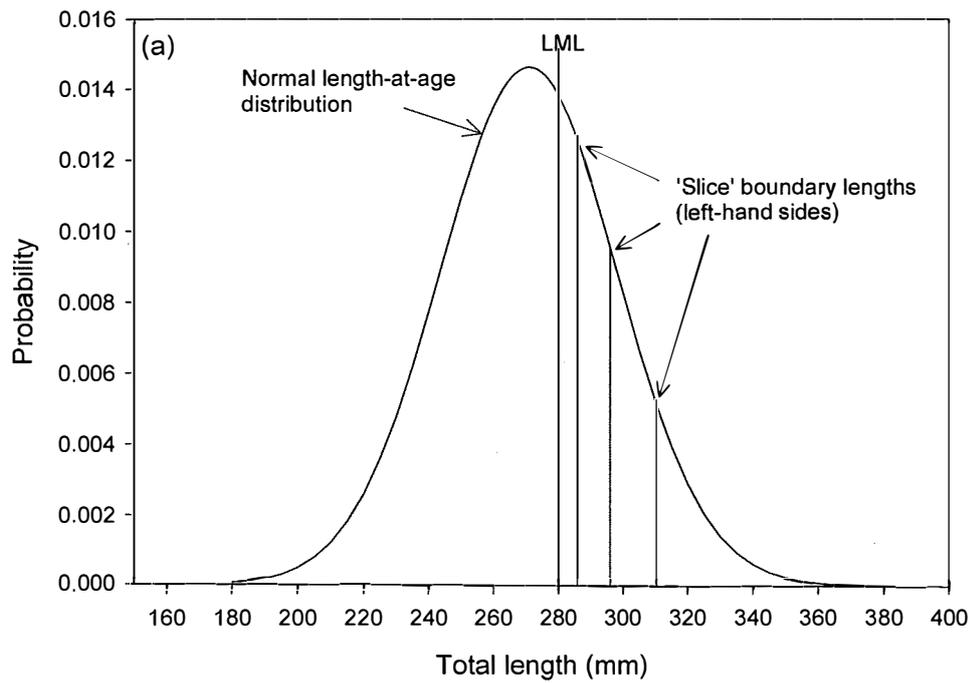


Figure 10.1. Example of length-slice decomposition of a normal cohort crossing LML. (a) The probability, i.e. proportion of the cohort, assigned to each slice is the newly added proportion greater than LML in each monthly age of growth. (b) In monthly model time steps subsequent to slice creation, numbers of fish surviving exploitation in slice are accounted for separately in the population array.

This provides a relatively computationally efficient age and length growth description. Length bins differentiate proportions of the cohort that cross LML in each monthly age. It uses the minimum number of length subintervals, one slice for each monthly time step of new recruits. We shall use this slice description only for cohort ages where the fitted normal has at least 2% on either side of the LML, and will denote these as ‘crossing’ cohorts. “Sublegal” cohorts are those for which 2% of the normal length-at-age distribution has not reached LML. “Postlegal” cohorts are those for which 98% or more have crossed LML.

A second computation saving is that much of the growth calculation can be carried out once ahead of model time step iteration. The intervals defining each slice are used as integral limits in calculating the means for weight and if needed, length, in each slice and cohort. These means were then calculated exactly. By assuming that growth does not vary in time, i.e. that the length distribution of each age (and each sex in each region) remains constant, no growth transition matrix, mean length formula such as von Bertalanffy, or functional assignment of lengths to weights were required. Mean ‘slice weights’-at-age and postlegal cohort weights-at-age were calculated as numerically integrated subintervals over the normal length-at-age distribution of each cohort. The slice and cohort weights were then read into the fishery stock assessment model estimation as fixed constants requiring no further calculation.

The algorithm for generating the slices which incorporates the (2%) cutoff minimum for the upper and lower tail slices, and which yields a slice partition that is complete (summing to 1) is presented in the Appendix to this chapter.

10.3 Results

The slice generation algorithm was implemented for all 6 data sets. Examples are tabulated for the case of Gulf St. Vincent females under a LML of 280 mm. Note that the number of slices depends on the month of age of the cohort. For example a crossing legal cohort that has legal components for 4 months (Table 1, Age 26 months) will have 4 legal slices. Slice number 1 is defined to be the first slice to have crossed into legal lengths, slice number (islice =) 2, the second legal slice created, and so on. Note also that all the slice boundaries (Table 10.1) change each month, i.e. a new slice partition above LML is needed with each monthly movement of the length at age distribution. Number of slices depends on the age of the cohort. For example, if the cohort has had a 2% proportion greater than LML for 5 months, there will be 5 slices generated.

Table 10.1. Left-hand length boundaries for each slice length subinterval: Gulf St. Vincent females, LML = 280 mm.

Age (months)	Month legal	Slice number														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
23	1	280														
24	2	294.23	280													
25	3	304.39	290.15	280												
26	4	310.30	296.05	285.89	280											
27	5	312.71	298.45	288.29	282.40	280										
28	6	313.09	298.83	288.68	282.78	280.38	280									
29	7	313.39	299.13	288.97	283.08	280.68	280.30	280								
30	8	315.54	301.27	291.11	285.21	282.82	282.43	282.14	280							
31	9	320.88	306.61	296.44	290.54	288.14	287.75	287.46	285.32	280						
32	10	329.73	315.44	305.26	299.35	296.94	296.56	296.26	294.12	288.80	280					
33	11	341.23	326.91	316.71	310.79	308.39	308.00	307.70	305.56	300.23	291.42	280				
34	12	353.74	339.40	329.18	323.25	320.84	320.45	320.15	318.01	312.66	303.83	292.39	280			
35	13	365.49	351.11	340.88	334.93	332.52	332.13	331.83	329.68	324.33	315.48	304.02	291.60	280		
36	14	375.09	360.69	350.44	344.48	342.06	341.68	341.38	339.22	333.86	325.00	313.52	301.08	289.46	280	
37	15	381.85	367.44	357.17	351.21	348.78	348.40	348.10	345.94	340.57	331.69	320.20	307.74	296.11	286.64	280

Table 10.2. Weight in kilograms of an average fish in each age and slice. Gulf St. Vincent females, LML = 280 mm.

Age (months)	Month legal	Slice number														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
23	1	0.145														
24	2	0.168	0.135													
25	3	0.187	0.151	0.133												
26	4	0.198	0.161	0.142	0.130											
27	5	0.203	0.165	0.146	0.133	0.127										
28	6	0.204	0.166	0.146	0.134	0.128	0.126									
29	7	0.204	0.166	0.147	0.135	0.128	0.126	0.126								
30	8	0.209	0.170	0.150	0.138	0.132	0.130	0.129	0.127							
31	9	0.220	0.180	0.159	0.146	0.140	0.137	0.137	0.135	0.130						
32	10	0.239	0.196	0.174	0.161	0.154	0.151	0.151	0.149	0.143	0.132					
33	11	0.266	0.220	0.196	0.181	0.173	0.171	0.170	0.168	0.162	0.150	0.135				
34	12	0.297	0.247	0.221	0.205	0.197	0.194	0.193	0.191	0.184	0.171	0.154	0.136			
35	13	0.329	0.275	0.247	0.229	0.220	0.218	0.217	0.214	0.207	0.193	0.174	0.154	0.135		
36	14	0.356	0.299	0.270	0.251	0.241	0.238	0.237	0.235	0.226	0.212	0.192	0.170	0.150	0.133	
37	15	0.377	0.317	0.286	0.267	0.257	0.253	0.253	0.250	0.241	0.226	0.205	0.182	0.161	0.144	0.131

Table 10.3. Portion of fish in slice as a proportion of total normal length-at-age cohort (Pslice) and as a proportion of the sublegal component (Psublegslice). Gulf St. Vincent females, LML = 280 mm.

Age (months)	Month legal	Pslice	Psublegslice
23	1	0.074	0.074
24	2	0.104	0.112
25	3	0.113	0.137
26	4	0.078	0.110
27	5	0.034	0.053
28	6	0.005	0.009
29	7	0.004	0.007
30	8	0.031	0.052
31	9	0.077	0.139
32	10	0.125	0.260
33	11	0.140	0.394
34	12	0.108	0.501
35	13	0.059	0.551
36	14	0.026	0.534
37	15	0.022	1.000

10.4 Discussion

The majority of fishery models fitting to catches-at-age are age-based, i.e. they do not further partition the population into lengths of the harvested fish in each age group. With King George whiting this additional independent variable of the model fish population was undertaken to describe monthly as opposed to merely yearly time change of the population.

The data warranted this level of detail. Monthly changes in catch are hypothesised to be associated with the growth of the new recruits to legal size in autumn and the shift of effort to King George whiting in autumn and early to mid-winter. By summer (December-January) the bulk of the new recruits are depleted and effort shifts to other species. The monthly data of catch and effort totals allow the possibility of capturing the depletion of the cohort by month. Because few fish survive a full year in the legal stock, and of those many migrate away from the principal fishing grounds, the

comparison of numbers in successive yearly ages, say 3 to 4, contain relatively coarse information about fishing mortality. Quantifying the depletion over monthly time steps is the sensible alternative.

Furthermore, the growth of fish across legal minimum length requires the slice description formulated above. Fishing mortality rates are sufficiently high that, of the fish in a given age class, most of the faster growing individuals are harvested by the time the slower growing ones reach LML. Monthly new recruits are the targeted sub-stock. To capture the growth process for modelling the fishery, both the mean weight of individuals harvested for fitting to catch totals (reported in kg) and the age-specific numbers captured by month for fitting to catch-at-age samples which are strongly affected by this arrival of recruits to legal size, the breakdown of each age class by length provides a substantially more accurate description of the harvested population.

This slice growth description should improve model accuracy relative to a purely age-based description for any fish stock where age class depletion is better reflected over monthly time scales, or where the numbers of new fish monthly crossing over (a knife-edge) LML are the majority or an important component of the fishable stock.

This age- and length-based growth submodel will be incorporated into the overall fishery estimator, fitting to catch and effort monthly totals, and month-specific catches-at-age, presented in Chapter 12.

10.5 Appendix: Algorithm for generation of cohort slice length partition

The principal inputs to the creation of the slice partition are the 8 parameters (θ) describing the normal length-at-age distribution for monthly age. These were derived in Chapter 9. The full probability density specifying the proportion in any length interval, including both legal and sublegal size fish, will be denoted $P(l | \theta; a)$, where the parameters of θ specify the mean and standard deviation of the normal spread of lengths, l , of King George whiting in each age, a . Six such parameter sets were obtained, for the 2 sexes and 3 regions of growth in South Australia. Recall that the mean was given by an exponent-generalised seasonal von Bertalanffy formula (Chap. 9, Eq. 3), and the standard deviation (Chap. 9, Eq. 2b) varied linearly and seasonally with age.

The goal of this calculation is twofold: To generate values for (i) the proportion of total fish in each newly created slice as a proportion of the fish in the sublegal component from which they are taken, and (ii) the mean weight of each legal slice of fish, and of each postlegal (whole) cohort, in each month. These inputs are used in the overall fishery estimation (Chapter 12) for (i) creating the new slice of legal size fish in each month, and (ii) in summing model catches by number to give catch totals by weight, one of two principal data sources to which the model is fitted.

We recall that the cohort ages of model King George whiting were divided into three categories: 'sublegals', those ages before the stock reaches LML, 'crossing legals', the ages when part of the cohort length-at-age distribution lies in sublegal and part in the legal range of lengths, and 'postlegals', ages when the cohort is designated to be of fully legal size.

In order to consider only 'crossing' cohorts, i.e. only ages in which meaningful proportions of the cohort lie on both sides of LML, slice probabilities of 2% and 98% were chosen as cut-offs. The first step, therefore was to identify and integrate over the normal density tails for the youngest and oldest ages, i.e. right- and left-hand tails respectively, that first satisfied the 2 and 98% thresholds. Define the larger part of the cohort that is of legal size in monthly age as $P_{leg}(a)$:

$$P_{leg}(a) = \begin{cases} 0, & \text{at age } a \text{ if } \int_{LML}^{\infty} P(l | \theta; a) dl < 0.02 \\ 1, & \text{at age } a \text{ if } \int_{LML}^{\infty} P(l | \theta; a) dl > 0.98 \\ \int_{LML}^{\infty} P(l | \theta; a) dl & \text{otherwise.} \end{cases} \quad (10A.1)$$

A 'slice' is the portion of legal KGW entering the fishable stock, by growing across the LML, in any given month. It was obtained as the proportion of the length-at-age cohort that is legal in the current month of age (a) minus the proportion that was legal the month of age preceding ($a - 1$). These were calculated for all ages (noting $P_{leg}(0) = 0$):

$$Pslice(a) = P_{leg}(a) - P_{leg}(a-1), \quad a = 1, \dots, \max(a). \quad (10A.2)$$

The sum of $Pslice(a)$ over all ages equals 1. The critical ages that specify when the cohort was 'crossing', call them a_{lc} and a_{fc} , are given by the youngest and oldest ages when $Pslice(a)$ is not equal to 0, in other words, the ages when more than 2% and less than 98% of the cohort straddled LML.

The new-slice proportions specified as a ratio over the sublegals and defined only for crossing ages, the desired outputs (i) above, are thus obtained as

$$Psublegslice(a) = \frac{Pslice(a)}{1 - P_{leg}(a-1)}, \quad a = a_{lc}, \dots, a_{fc}. \quad (10A.3)$$

Note (Table 10.3) that the intuitive values for a_{lc} and a_{fc} were obtained, namely, $Psublegslice(a_{lc}) = Pslice(a_{lc})$ since all of the cohort was sublegal in the month of age preceding a_{lc} , and $Psublegslice(a_{fc}) = 1$, since all the remaining sublegals must become legal in the oldest 'crossing' age.

To derive (ii) the mean weights of each slice, we need the length subintervals defining each 'slice', and a mean-weight-versus-length relationship. The latter was given in Chapter 9.

With each increasing crossing-legal month of age, the number of slices increases by 1 and is equal to the number of months of age the cohort has had a legal component greater than 2%. Call this number of slices $n_s(a)$:

$$n_s(a) = a - a_{lc} + 1, \quad a = a_{lc}, \dots, a_{fc}. \quad (10A.4)$$

In the model population array, slices were enumerated starting with $islice = 1$ for the first crossing slice to be created, at age a_{lc} . At higher ages, $islice = 1$ continued to refer to this same largest slice, $islice = 2$ identifies the second largest slice, and so on.

At the first (i.e. youngest) crossing age, the left-hand-side of the (single) slice subinterval is LML. We can notate this as $Lhs[age=a_{lc}, islice=1] = LML$. Likewise, for all crossing ages except the last,

i.e. for $a = a_{1c}, \dots, a_{fc} - 1$, $Lhs[a, islice=n_s(a)] = LML$, since the left-hand-side of all newly created slice subintervals is LML.

All other slice left-hand sides were obtained to be consistent with the $Pslice(a)$ probabilities defined in Eq. 10A.2, i.e. in such a way that the probabilities under each slice subinterval equalled the probability values already assigned as each slice was created, which do not change with increasing age of the crossing cohort. For example consider the right-hand tail slice, $islice = 1$, at the second legal monthly age (which as noted, will have 2 legal slices, the other newly created slice, $islice = 2$, having LML as its left hand side). The left-hand side $Lhs[age=a_{1c}+1, islice=1]$ was obtained by numerically solving for the left-hand integration limit in the integral equation,

$$Pslice(a_{1c}) = \int_{Lhs[a_{1c}+1, 1]}^{\infty} P(l | \theta; a_{1c} + 1) dl .$$

For all higher crossing cohort ages, and all slices in each age except the newly created ones, a similar integral equation was numerically solved to derive $Lhs[a, islice]$. The crossing month when each slice was created is given by $(a_{1c} - 1 + islice)$, thus

$$Pslice(a_{1c} - 1 + islice) = \int_{Lhs[a, islice]}^{Lhs[a, islice-1]} P(l | \theta; a) dl \quad (10A.5)$$

for ages, $a = a_{1c+1}, \dots, a_{fc}$ and $islice = 1, \dots, n_s(a)-1$. Because the upper integration bound, $Lhs[a, islice-1]$ is given by each previous successive solution, derived as the left-hand side of the slice immediately to its right, $islice-1$, these integral equations for successive slices were solved iteratively starting with the right-hand tail slice ($islice = 1$) and progressing to the left.

These left-hand side values were employed to specify integration limits on the length axis for calculating mean weight in each slice:

$$w[a, islice] = \int_{Lhs[a, islice]}^{Lhs[a, islice-1]} \alpha l^\beta P(l | \theta; a) dl . \quad (10A.6)$$

Similar integrations were carried out to calculate mean weights for the normal 'postlegal' cohort length-at-age distributions, which are not subdivided by slice.

There were 12 slice-growth output files generated, one for each sex (2), region (3), and LML (2).

CHAPTER 11. ESTIMATING RATES OF MOVEMENT AMONG MODEL SPATIAL CELLS.

R. McGarvey and J. Feenstra

11.1 Introduction

It was shown in Chapters 5 and 6 that movement of King George whiting is an important aspect of its life-history. Spawning occurs near the entrances to the two gulfs, after which eggs and larvae are thought to be transported passively into and around the gulfs. Post-larvae settle into shallow embayments, seagrass beds, and other near-shore habitats in the upper reaches. As fish reach the age of 3 years, approximately the age when they become both mature and legally susceptible to harvesting, they range more widely and many undergo directed migration southward (Chap. 6). By age 4 few fish remain available to the fishery in these areas. Spawning occurs only in specific areas around the southern parts of the gulfs. Thus, the reproductive population is sustained by active movement of adults southward to spawning aggregations, and passive transport of larvae back to nursery areas in the gulfs.

Adult movement is also an essential feature of the fishery. During the time between reaching legal size (280 mm prior to September 1995, 300 mm thereafter) and migration into deeper water for spawning, South Australian King George whiting are subjected to high rates of exploitation. Jones et al. (1990) estimated total mortality rates (Z) in the mid 1980's at from 1 to 3.2 in the inshore coastal waters where the majority of the catch is taken. Rates of exploitation in southern locations where spawning occurs are lower. This led to the idea that the King George whiting fishery is a 'gauntlet' fishery, and that sustainability under such high levels of exploitation is possible because the spawning aggregations are also effective partial refuges. Thus, to model the ability of the population to persist at current levels of harvesting, it is necessary to divide up the population into regions which differentiate spawning grounds from the main inshore fishery.

For modelling this stock, explicit representation of adult movement is necessary for a second reason. When movement is not explicit, estimates of mortality will be biased. Rates of exploitation are inferred from the decline in relative numbers in successive ages from catches-at-age or from tag time-at-large. Lower abundances at higher ages are assumed to have resulted from natural deaths or harvesting. This is true of most mortality estimation methods. By representing emigration as an additional source of depletion in the upper gulf fishery zones (and of immigration into lower gulf spawning aggregations), this source of pseudo-mortality is explicit and the bias thereby alleviated or reduced.

Qualitative patterns of movement were investigated in Chapter 6 using tag recaptures from commercial and recreational fishers. To incorporate migration into the overall fishery model estimation (from which recruitment and exploitation rate will be estimated from catch data and catches-at-age in Chapter 12), the rates of movement among cells must be estimated quantitatively. Here, a reduced subset of the tag-recapture data set was employed to carry out the estimation of movement rates.

11.2 Methods

The movement model assumed movement at one time each year. Data sample sizes were not sufficient to subdivide the recaptures into smaller time intervals than 1 year. Qualitative examination of tag recaptures by seasons indicated that most directed movement occurred in summer, though some movement, including some northward drift alongshore in Gulf St. Vincent, occurred in all seasons (Chpt 6). Because summer appeared to be the time of active migration, and because directed migratory movement southward in the gulfs was the feature we sought to capture in the model, the movement was programmed to occur at the model time step at the beginning of January.

The spatial cells of the King George whiting model were chosen to represent and quantify the movement trends mapped in Chapter 6. The catch and effort data to which the overall stock assessment model will be fitted is reported for 1 degree squares known as Marine Fishing Areas or 'MFA blocks' (Fig. 2.1). There are approximately 27 MFA blocks with significant King George whiting catch. To reduce model complexity and subdivide the fishery into model cells of number appropriate to the movement tag-recapture sample size (453), MFA blocks were aggregated into 12 movement cells (Fig. 11.1). Model cell 13 comprises all outlying, mostly offshore blocks where reported catches of King George whiting are small (0.14%) and from which no tag recoveries were obtained.

A 14th cell was added to accommodate the lack of knowledge of reproduction from the West Coast (Chpt 4). Though the spawning grounds for populations on the West Coast are to date unidentified, we assume that these locations exist, or at least that the near absence of fish greater than age 3, and virtual absence of fish greater than age 4 in the catch samples, together with the absence of any actively spawning individuals in the commercial catch from the West Coast (Chpt 3), implies that fish do move offshore to spawn. The hypothetical locations for spawning on the West Coast were allocated to a theoretical model cell number 14.

Movement to West Coast spawning cell 14 was inferred from the absence of older fish in the inshore commercial catch. The estimation of movement rates to this hypothetical cell 14 from the three

inshore West Coast cells was thus carried out in the overall King George model estimator (Chpt 12) where catch and effort totals and sampled catches by age are inputs.

Movement in the model is represented by a transition matrix. There are 12 model movement cells and thus 12 possible 'destination' cells from each model 'source' cell. At each yearly time of movement, the model fish population in each cell are apportioned, moving to one of the other cells or remaining in the source cell. From each cell, the probabilities of moving to any other cell or of remaining in the source cell must sum to 1. This vector of movement from any given source cell is written as a column of probabilities. Thus the elements in each column sum to 1. There are 12 columns of probabilities to model movement from each model cell. The movement of fish of a particular age on January 1 of each year can thus be summarised by a matrix of probabilities, P_{ji} .

The rates of movement vary with age. King George whiting cohorts are defined to be age 1 month in the peak spawning month of May. We considered two January ages explicitly in the estimation, 33 months and 45 months of age. Thus there are two matrices of movement probabilities to estimate, $P_{1,ji}$ and $P_{2,ji}$, corresponding to these two ages.

Movement at January ages greater than 45 months (57 months, 69 months, etc.) was assumed to follow the matrix, $P_{2,ji}$, estimated for the 45 month-old fish. Very few tags or even recaptures are available for fish older than 45 months, and the migratory down-Gulf movement behaviour of King George whiting appears to be fully expressed in the 45-month-old fish.

Because the sex of recaptured fish is not known (which would require dissection and examination of gonads, not undertaken by fishers who report recaptures), the same two matrices will be applied to both sexes of the population variable in the overall King George whiting estimator of Chapter 12.

For estimating the movement probability parameters, only recaptured fish which had an 'opportunity' to undertake movement at the January movement time will be considered. Each data point, that is each tagged recaptured fish, was classified by whether it crossed the January 1 movement time once at 33 months, once at 45 months, or twice at both 33 and 45 months of age. Only fish recaptures from these three time-at-large categories, i.e. those fish in the water long enough to cross January 1, were included in the movement estimation likelihood.

In addition, we excluded recaptures that were not tagged at least two months prior to January 1, i.e. which were tagged during the principal migration months of November and December, which might have already undertaken summer migratory movement before tagging. Other sets of exclusion criteria

were also tested, in particular those which required a 6-month time-at-large prior to May 1, but these excluded many more data points without appearing to result in greater numbers that moved between cells. In addition, using the January movement time and 2-month minimum time-at-large criteria, the mean time at large for an average tag recapture was approximately a full year.

Classification of recapture data points into the three time-at-large movement cases was specified by the months of age when the fish was tagged and recaptured (Table 11.1). October is month 30 for 2-year olds, and month 42 for 3 year olds. The three cases are abbreviated as follows: (2T1) crossing January once at 33 months of age, (3T1) once at 45 months of age, and (2T2) at both 33 and 45 months.

Table 11.1. Tag interval and recapture age interval (in months) defining each category of time-at-large case for analysis of movement.

Data point case abbreviation	Tag release age interval		Recapture age interval		Sample Size
	Start month	end month	start month	end month	
2T1	1	30	33	44	329
3T1	31	42	45	∞	101
2T2	1	30	45	∞	23

Total recaptures with tag and recapture locations reported were 2054, of which 453 fell into one the three cases, crossing January, employed in the movement estimation (Table 11.2).

Table 11.2. Tag recapture data used in the estimation of movement rates among 12 movement cells of the King George whiting model. Numbers recaptured in matrix elements N_{ji}^r for (a) crossing January once at age 33 months (2T1); (b) crossing January once at age 45 months (3T1); (c) crossing January twice at ages 33 and 45 months (2T2).

(a)

Destination spatial cell	Source spatial cell											
	1	2	3	4	5	6	7	8	9	10	11	12
1	49	1	1	0	0	0	0	0	0	0	0	0
2	0	41	2	0	0	0	0	0	0	0	0	0
3	0	0	53	0	0	2	0	0	0	0	0	0
4	0	0	0	6	0	9	0	0	0	0	0	0
5	0	0	0	0	28	18	0	0	0	0	0	0
6	0	0	0	0	0	25	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	1	1	0
8	0	0	0	0	0	0	0	23	0	4	2	0
9	0	0	0	0	0	0	0	0	4	3	8	0
10	0	0	0	0	0	0	0	0	0	22	2	0
11	0	0	0	0	0	0	0	0	0	6	16	0
12	2	0	0	0	0	0	0	0	0	0	0	0

(b)

Destination spatial cell	Source spatial cell											
	1	2	3	4	5	6	7	8	9	10	11	12
1	9	0	0	0	0	0	0	0	0	0	0	0
2	0	3	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	8	0	14	0	0	0	0	0	0
5	0	0	0	0	1	1	0	0	0	0	0	0
6	0	0	0	1	0	20	0	0	0	0	0	0
7	0	0	0	0	0	0	0	2	0	0	3	0
8	0	0	0	0	0	0	0	18	1	4	2	0
9	0	0	0	0	0	0	0	0	2	2	4	0
10	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	6	0
12	0	0	0	0	0	0	0	0	0	0	0	0

(c)

Destination spatial cell	Source spatial cell											
	1	2	3	4	5	6	7	8	9	10	11	12
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	1	0	4	0	0	0	0	0	0
5	0	0	0	0	1	9	0	0	0	0	0	0
6	0	0	0	0	0	1	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	1	1	0
8	0	0	0	0	0	0	0	1	0	1	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	2	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0

One of the principal drawbacks of migration estimation using tag recoveries by commercial and recreational fishers is that many, probably a majority, of recaptured tagged fish are not reported to fishery researchers who compile the database. Thus absolute numbers recovered from each cell as a fraction of the numbers released do not provide meaningful information. By implication, the original number tagged is not directly useful. Rather, the principal information about movement from tag recoveries is the *relative* numbers recaptured and reported in each destination cell j of all recaptured fish that were released from any given source cell i . The model likelihood of this movement estimator was fitted to these observed relative proportions.

However, to derive these model-predicted proportions, as a logical starting point, equations were derived for the absolute number of recaptures, as a function of the number tagged. When proportions recovered in each destination cell are formed, the numbers tagged cancel. Numbers recaptured depend not only on movement. The predicted number recaptured in each destination cell of those released in each source cell is written below as a product of probabilities for tagging mortality, survival, movement, death, capture, and tag reporting.

Because survival is a strongly non-linear (negative exponential) function of time-at-large in the time periods before and after the hypothesised time(s) of movement, the months of tagging (a_t) and recapture (a_r) needed to be explicit.

In Eq. 11.1 below, the predicted absolute number reported recaptured in cell j in month a_r , that were released in cell i in month a_t , equals the number originally tagged and released in cell i in month a_t , times the proportion surviving tag mortality in the short time (approximately a month) following tagging, times the fraction surviving total mortality over the months from tagging to the assumed time

of possible movement (a_m), times the probability of moving from cell i to cell j , times the subsequent survival from month of movement to month of recapture, times the probability of dying in the month of recapture, times the probability that the cause of death was harvest, times the probability that the captured fish was reported.

Given prior estimates for fishing mortality (F_j) and total mortality (Z_j) in each of the cells, j , the movement rate probabilities $P_{a_m,ji}$ are the sole remaining unevaluated parameters. These were obtained by maximising the likelihood described below.

Thus the equation for predicted number of recaptures, for the two cases (2T1 and 3T1) of recaptures whose time-at-large traversed the assumed time of movement (January 1) only once, can be written:

$$\hat{N}_{ji,a_r,a_t}^r = N_{i,a_t}^t \cdot (1 - m_{tag}) \cdot S_i[a_m - a_t] \cdot P_{a_m,ji} \cdot S_j[a_r - a_m] \cdot (1 - e^{-Z_j/12}) \cdot (F_j / Z_j) \cdot f_{report} \quad (11.1)$$

where

- $\hat{N}_{ji,a_r,a_t}^r \equiv$ Predicted number of recaptures of fish in spatial cell j of age (in months) a_r that were released and tagged in spatial cell i at age a_t .
- $N_{i,a_t}^t \equiv$ Number of fish tagged in spatial cell i at age a_t .
- $m_{tag} \equiv$ Mortality due to tagging. This component of tag mortality is taken as a fixed proportion, and is assumed to occur shortly after tagging.
- $a_m \equiv$ Ages at month of movement (January). $a_m \in \{a_{m1} = 33, a_{m2} = 45\}$.
- $a_t \equiv$ Age at which a given (data recapture) fish was tagged.
- $S_i[a_m - a_t] \equiv$ Probability of a fish tagged at age a_t in spatial cell i surviving to age a_m (while remaining in spatial cell i).
- $P_{a_m,ji} \equiv$ Probability of movement at age a_m from spatial cell i to spatial cell j .
- $a_r \equiv$ Age at which a given fish was recaptured.
- $S_j[a_r - a_m] \equiv$ Probability of a fish alive after time of movement at age a_m in spatial cell j surviving to age a_r in spatial cell j .
- $F_j \equiv$ Instantaneous mortality rate, for fish in spatial cell j , due to fishing from which recaptures can be obtained.
- $f_{report} \equiv$ Average fraction of recaptured tagged fish that were reported.

If the recaptures cross over 2 times of movement, Eq. 11.1 generalises to:

$$\hat{N}_{j_i, a_i}^r = N_{i, a_i}^t \cdot (1 - m_{\text{tag}}) \cdot S_i[a_{m1} - a_i] \cdot \left\{ \sum_{k=1}^{n_c} P_{1,ki} \cdot S_k[a_{m2} - a_{m1}] \cdot P_{2,jk} \right\} \cdot S_j[a_i - a_{m2}] \cdot \left(1 - e^{-Z_j/12}\right) \cdot (F_j/Z_j) \cdot f_{\text{recapt}} \quad (11.2)$$

where,

- $n_c \equiv$ Total number of spatial cells (= 12).
- $a_{m1} \equiv$ The first defined age of movement in the model, month of age 33. The P-matrix of movement probabilities for fish of this age will also be identified by a subscript of 1.
- $a_{m2} \equiv$ The second age at which fish can migrate in the model, January month of age 45. P-matrix subscript of 2.

We approximated the probability of death in any month, $(1 - e^{-Z_j/12})$ by $Z_j/12$, the first order Taylor expansion. This approximation is acceptable for total mortality rates, Z_j , of order 1 or less. (For example, with $Z = 1.0$, $(1 - e^{-Z/12}) = 0.080$ and $Z/12 = 0.083$.) This approximation simplifies Eqs. 11.1 and 11.2 by allowing the first-order Z_j in $(1 - e^{-Z_j/12})$ to cancel with the factor (F_j/Z_j) for probability that the death is due to capture.

Estimates of Z_j can be obtained by two methods. For the initial set of estimates whose values are presented in the Results section below, we estimated Z in each cell, j , as the reciprocal of mean time at large (Gulland 1955; Chapman 1961) of tag recaptures that remained in cell j . Two liabilities of this method inhere: (1) This tag time-at-large estimator has a large variance, and as noted in the Introduction, (2) would be biased by not explicitly considering movement away from each cell.

For these two reasons, a second set of Z_j and F_j estimates were used, obtained from the overall King George whiting estimator (Chpt 12). These were derived for the final analysis of movement probabilities after iterating back between the movement estimator and the overall fishery estimator.

The explicit form for the survival factor, S , between any two monthly ages a_1 and a_2 is

$$S_j[a_1 - a_2] = e^{-Z_j(a_2 - a_1)/12} \quad (11.3)$$

The Z_j estimates assume a yearly time unit. Division by 12 in Eq. 11.3 converts monthly $(a_2 - a_1)$ into yearly time.

The predicted proportions, f_{ji} , for the case of recaptures whose time at large spans the first movement age, month 33, are:

$$f_1(j \mid i, a_t, a_r) = \frac{\hat{N}_{ji, a_r, a_t}^r}{\sum_{k=1}^{n_c} \hat{N}_{ki, a_r, a_t}^r} \quad (11.4)$$

Once Eq. 11.1 is substituted into Eq. 11.4, the constant factors $(1 - m_{tag}, 1/12, \text{ and } f_{report})$ in the model equation will cancel. The numbers tagged in cell i , N_{i, a_t} , and the survival factors for the time from tagging to movement, $S_i[a_{m1} - a_t]$, will also cancel since all data points in the proportion calculated were tagged in spatial cell i , and survived to reach the assumed time of migration, a_{m1} .

Substituting Eq. 11.2, f_i (case 2T1) reduces to

$$f_1(j \mid i, a_r) = \frac{P_{1, ji} \cdot S_j[a_r - a_{m1}] \cdot F_j}{\sum_{k=1}^{n_c} P_{1, ki} \cdot S_k[a_r - a_{m1}] \cdot F_k} \quad (11.5)$$

With a_t no longer explicit, this is the predicted proportion recaptured in cell j , in month a_r of those released in cell i , for any tag month a_t falling into this case. Similarly with cases 3T1 and 2T2 below.

For the case (3T1) of recaptures whose time at large spans the second movement age, month 45, the proportions recaptured from each cell j in month of age a_r , of those recaptures released from cell i in month a_t become

$$f_2(j \mid i, a_r) = \frac{N_{ji, a_r, a_i}^r}{\sum_{k=1}^{n_c} N_{ki, a_r, a_i}^r} = \frac{P_{2, ji} \cdot S_j[a_r - a_{m2}] \cdot F_j}{\sum_{k=1}^{n_c} P_{2, ki} \cdot S_k[a_r - a_{m2}] \cdot F_k} \quad (11.6)$$

For the 2T2 case of recaptures whose time at large spans two movement ages, $a_{m1} = 33$ months and $a_{m2} = 45$ months, the predicted proportion recaptured in cell j in month a_r of those tagged in cell i is:

$$f_{1\&2}(j \mid i, a_r) = \frac{\left\{ \sum_{l=1}^{n_c} P_{1, li} \cdot (S_l[a_{m2} - a_{m1}] \cdot P_{2, jl}) \right\} \cdot S_j[a_r - a_{m2}] \cdot F_j}{\sum_{k=1}^{n_c} \left\{ \sum_{l=1}^{n_c} P_{1, li} \cdot (S_l[a_{m2} - a_{m1}] \cdot P_{2, kl}) \right\} \cdot S_k[a_r - a_{m2}] \cdot F_k} \quad (11.7)$$

The sum represents the possible pathways of movement from cell i before the first yearly movement and reaching cell j after the second. In the first movement time, the fish may move to any cell l and in the second must move from that intermediary cell to cell j . The probabilities of each pathway are (1) movement from cell of tagging i to any cell l with probability $P_{1, li}$, (2) survival in l over the full year from a_{m1} to a_{m2} , and (3) movement from intermediate cell l to recapture cell, j . In matrix multiplication formulations of this expression, the order of movement matrix multiplications is written in inverse order as $P_{2, jl} \cdot P_{1, li}$.

For observed cell of tagging, i , if recaptured in month a_r , the f 's over j form a set of discrete probabilities (probability mass function, pmf) for the set of possible outcomes, namely the possible cells, j , in which the fish will be recaptured.

The overall movement estimation joint likelihood is thus the product of the predicted pmf probabilities for each observed outcome, the product of the f 's:

$$L = \prod_{r=1}^{n_r} f[r] \quad (11.8)$$

where r is the index over fitted recapture data points, of which there are n_r .

The objective function, the minus log likelihood,

$$O = - \sum_{r=1}^{n_r} \log(f[r]) \quad (11.9)$$

was minimised by varying the movement parameters, $\{P_{s,ji}; s \in \{1, 2\}; i, j \in \{1, n_c\} \}$ that we seek to estimate.

To assure that the probabilities all summed (over j) to 1, the parameters were constrained with the added penalty objective function term of

$$\sum_{s=1}^2 \sum_{i=1}^{n_c} \left[\log \left(\sum_{j=1}^{n_c} P_{s,ji} \right) \right]^2 . \quad (11.10)$$

This will equal 0 if all the columns (i) in both of the estimated transition matrices (s), are all 0, and increase to a positive value for any column that deviates above or below a sum of 1. Thus minimising the objective function will be achieved by obtaining properly normalised probabilities.

Additional individual constraints were imposed on the $2 \cdot (n_c)^2$ parameters to assure that they are all ≥ 0 by limiting the search algorithm to non-negative values.

The objective function was programmed and minimised using AD Model Builder, a model estimation software developed by D.A. Fournier, which uses derivatives evaluated using the reverse auto-differentiation algorithm. This allows rapid convergence to the minimum solution. Runs with 453 data points and $2 \cdot 144$ parameters in the likelihood converged in about 2 minutes.

11.3 Results

Four overall trends are apparent in the estimated matrices (Table 11.3) of movement probabilities, $P_{1,ji}$ and $P_{2,ji}$.

Table 11.3. Estimated movement probabilities: (a) $P_{1,ji}$ (age 33 months), and (b) $P_{2,ji}$ (age 45 months), where row (j) designates destination model spatial cell, and column (i) the source cell.

(a)

Destination spatial cell	Source spatial cell											
	1	2	3	4	5	6	7	8	9	10	11	12
1	0.961	0.023	0.018	0	0	0	0	0	0	0	0	0
2	0	0.977	0.036	0	0	0	0	0	0	0	0	0
3	0	0	0.946	0	0	0.032	0	0	0	0	0	0
4	0	0	0	1.000	0	0.159	0	0	0	0	0	0
5	0	0	0	0	1.000	0.391	0	0	0	0	0	0
6	0	0	0	0	0	0.417	0	0	0	0	0	0
7	0	0	0	0	0	0	1.000	0	0	0.035	0.040	0
8	0	0	0	0	0	0	0	1.000	0	0.108	0.068	0
9	0	0	0	0	0	0	0	0	1.000	0.076	0.267	0
10	0	0	0	0	0	0	0	0	0	0.617	0.067	0
11	0	0	0	0	0	0	0	0	0	0.163	0.559	0
12	0.039	0	0	0	0	0	0	0	0	0	0	1.000

(b)

Destination spatial cell	Source spatial cell											
	1	2	3	4	5	6	7	8	9	10	11	12
1	1.000	0	0	0	0	0	0	0	0	0	0	0
2	0	1.000	0	0	0	0	0	0	0	0	0	0
3	0	0	0.0098	0	0	0	0	0	0	0	0	0
4	0	0	0	0.911	0	0.421	0	0	0	0	0	0
5	0	0	0.0002	0	1.000	0.034	0	0	0	0	0	0
6	0	0	0	0.089	0	0.545	0	0	0	0	0	0
7	0	0	0	0	0	0	1.000	0.101	0	0	0.260	0
8	0	0	0	0	0	0	0	0.899	0.345	0.540	0.125	0
9	0	0	0	0	0	0	0	0	0.655	0.230	0.246	0
10	0	0	0	0	0	0	0	0	0	0.230	0	0
11	0	0	0	0	0	0	0	0	0	0	0.369	0
12	0	0	0	0	0	0	0	0	0	0	0	1.000

First, from a majority of source cells, there is relatively little movement away, indicated by values equal to or near 1 on the diagonal of the movement transition matrix.

Second, most movement occurred from spatial cells 6, 10 and 11. These are the upper cells of the Spencer Gulf (6), and the Gulf St. Vincent (10 and 11) respectively. Thus nearly all significant movement was directed southward in the two Gulfs.

Third, the estimated rates were, in general, significantly higher for the 45-month-old (3 1/2-year-old) ($P_{2,ji}$) fish.

Fourth, there is virtually no movement between regions, corroborating the qualitative analysis of

Chapter 6.

Confidence bounds (Table 11.4) on the model parameters were estimated in AD Model Builder from the diagonal of the variance-covariance matrix, in turn estimated from the negative inverse of the Hessian evaluated at the likelihood maximum. These confidence bound estimates assume an asymptotic approximation by a multivariate normal of the likelihood versus parameter surface about the likelihood maximum.

Table 11.4. Standard errors calculated as the diagonal elements of the variance-covariance matrix, for the estimated movement probabilities of Tables 11.2a and 11.2b: (a) standard errors of P_{i,j_i} , and (b) standard errors of P_{2,j_i} .

(a)

Destination spatial cell	Source spatial cell											
	1	2	3	4	5	6	7	8	9	10	11	12
1	0.2213	0.0025	0.0037	0	0	0	0	0	0	0	0	0
2	0	0.1780	0.0075	0	0	0	0	0	0	0	0	0
3	0	0	0.2161	0	0	0.0105	0	0	0	0	0	0
4	0	0	0	0.0001	0	0.0511	0	0	0	0	0	0
5	0	0	0	0	0.0002	0.1221	0	0	0	0	0	0
6	0	0	0	0	0	0.1297	0	0	0	0	0	0
7	0	0	0	0	0	0	0.0032	0	0	0.0157	0.0265	0
8	0	0	0	0	0	0	0	0.0000	0	0.0489	0.0445	0
9	0	0	0	0	0	0	0	0	0.0004	0.0345	0.1738	0
10	0	0	0	0	0	0	0	0	0	0.2894	0.0437	0
11	0	0	0	0	0	0	0	0	0	0.0738	0.3567	0
12	0.0087	0	0	0	0	0	0	0	0	0	0	0.0091

(b)

Destination spatial cell	Source spatial cell											
	1	2	3	4	5	6	7	8	9	10	11	12
1	0.0004	0	0	0	0	0	0	0	0	0	0	0
2	0	0.0006	0	0	0	0	0	0	0	0	0	0
3	0	0	0.0390	0	0	0	0	0	0	0	0	0
4	0	0	0	0.3708	0	0.1525	0	0	0	0	0	0
5	0	0	0.0001	0	0.0003	0.0136	0	0	0	0	0	0
6	0	0	0	0.0359	0	0.1867	0	0	0	0	0	0
7	0	0	0	0	0	0	0.0013	0.0767	0	0	0.2005	0
8	0	0	0	0	0	0	0	0.6021	0.1344	0.2432	0.0970	0
9	0	0	0	0	0	0	0	0	0.2443	0.1104	0.1894	0
10	0	0	0	0	0	0	0	0	0	0.1104	0	0
11	0	0	0	0	0	0	0	0	0	0	0.2830	0
12	0	0	0	0	0	0	0	0	0	0	0	0.0108

11.4 Discussion

The two estimated matrices of movement transition probabilities, $P_{1,ji}$, and $P_{2,ji}$, yielded an outcome similar to that anticipated from the qualitative examination of the directional displacement of recaptures in maps of Chapter 6. The formal estimation analysis allowed the explicit consideration of variations in the amount of effort in different recapture cells (via the factor F_j), variations in survival rates among cells due to both month of recapture and spatial differences in overall levels of mortality, and permitted the combining of recaptures spanning two movement time periods with the two sets of recaptures that were at large crossing one January movement time. Most importantly it yielded a matrix of yearly movement transitions essential for modelling a migratory fish stock. A means to formally estimate movement transition probabilities remains an objective for several other Australian fish stocks, including southern Australian school shark.

This movement estimator offers the following features for use in fisheries modelling applications:

1. As noted, forming the expected observation as proportions of recaptures actually reported, (conditioning on recaptures, not numbers tagged) allows a considerable number of sources of bias to cancel out: numbers tagged, (short-term) tag mortality, survival from time of tagging to (first) time of movement, and the reporting rate.
2. The estimator can be applied to data sets where times of tagging and recapture are random rather than spaced apart by some discrete interval, usually a year. This requirement is common in scientist-conducted mark-recapture measurement of birds and other natural populations.

The ability to cancel away (an assumed constant) rate of non-reporting permits application to fishery tag-recovery studies, where the recaptures are nearly always reported by commercial and recreational fishers and substantial non-reporting is inevitable and where the timing of recaptures is random.

A number of approximations remain. These include

1. The assumption that movement happens once per year, in mid-summer.
2. The assumption that non-reporting is uniform in time and spatial cell.
3. The assumption that Z_j and F_j are constants. These can be estimated by the method of inverse time-at-large, which allows all the information needed for this estimator of movement rates to be obtained from the tag-recovery data set. Or they can be estimated, as we have done, from catches-at-age where the movements are explicitly taken into consideration.

Longer-term continuous tag loss is not explicit in Equation 11.1, and must be understood as implicitly incorporated as an added contribution to Z_j .

The resulting estimates were sensitive to the assumed total and fishing mortality rates in each recapture cell. Varying these revealed a measurable dependence of the movement rate estimates on the assumed levels of F_j in each recapture cell, j . These estimates of fishing mortality in each cell quantify the level of, and thus compensate quantitatively for variations in the amount of fishing effort used to recapture the tags reported in each recapture cell.

The best way to improve the accuracy of the F_j 's would be to integrate the movement estimation with the overall fishery estimator to be presented in Chapter 12. At current levels of computational power, this is not feasible. Therefore we constructed the fishery estimator of Chapter 12 using the estimated movement parameters as inputs. However as noted, we made one step towards integration by carrying out one movement-fishing mortality iteration: The F_j 's obtained from the run of the full estimator of Chapter 12 were sent back to the migration estimator and movement parameters derived again.

In practice, this substantially improved the accuracy and precision of the assumed F_j 's, in particular because the inputs to the Chapter 12 fishery estimation, catches by age and catch and effort totals, will provide a more precise measure of mean fishing mortality, F_j , in each cell j .

Overall, however, the relatively close agreement with the qualitative outcomes of Chapter 6, suggests that the spatial modelling of Chapter 12 will be satisfactorily represented by the movement transition matrices derived.

11.5 References

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CHAPTER 12. ESTIMATING PERFORMANCE INDICATORS FOR THE KING GEORGE WHITING FISHERY: A SPATIAL DYNAMIC MODEL INTEGRATING CATCH AND EFFORT, CATCHES-AT-AGE, AGE- AND LENGTH-BASED GROWTH, AND YEARLY MOVEMENT.

R. McGarvey and J. Feenstra

12.1 Introduction

The principal research goal of industry, specifically the Marine Scalefish Fishery Management Committee, as outlined in the South Australian Fisheries and Aquaculture Five Year Research and Development Strategy completed in June 1998, is to provide yearly indicators of the changes in abundance, recruitment, and exploitation rate. PIRSA managers have reiterated this need for management decision making. The goal of this chapter is to present the model estimator developed under this FRDC project to achieve that management research objective. In addition, these model rate equations and the parameters to be estimated from this chapter will form the basis of the simulation underlying the management strategy evaluation model software of Chapter 13.

The data currently available from the fishery on reproductive biology, life-history, adult movement, growth, and age structure of the King George whiting population are considerable. These were gathered both under the current FRDC project and under relatively extensive on-going biological and fishery research since the 1960's (Jones et al. 1990).

The first principal data input is the monthly South Australian marine scale commercial catch and effort data. Fishers report both the gear type and the species that they target on each day. The trends in catch and effort were summarised in Chapter 8.

The second principal data set, catches-at-age from otoliths, were gathered and ages read under the current FRDC King George whiting project. These were summarised in Chapter 3. Samples were taken principally from commercial processors, but also from volunteer recreational and research field sampling, for a range of spatial cells and months, from April 1994 to May 1998. This yielded 194 distributions of sampled catch-numbers-at-age, a total sample size of 10781 fish measured.

In Chapter 9, the seasonal generalised von Bertalanffy growth model with linear variation in standard deviation was fitted to lengths-at-age from the same set of otolith samples. These yielded (left-truncated) normal length-at-age distributions for every month of age, the fit undertaken for each sex and region.

The slice submodel of growth presented in Chapter 10 was then formulated from the distribution fits of Chapter 9 specifically for use in the King George whiting fishery model estimator presented below. Length-at-age distributions were partitioned by length for monthly ages where the length-at-age distribution straddles legal minimum length (LML), i.e. for the months of age when the cohort is entering the fishable stock. These we called 'crossing' cohorts. Most of the fishery's catch is taken from the crossing cohort ages because of the high levels of mortality on SA King George whiting and because the fishery targets the inshore subpopulation before it migrates offshore, about a year or less after reaching legal size. The length subintervals, created monthly, were called slices. Each slice represents the portion of the yearly cohort that grows (i.e. crosses) into legally harvestable size each month. The mean weight of each fish captured is more accurately predicted by this slice model description than if the mean weight of all fish in the cohort age were used. Furthermore, the numbers entering the fishable stock, particularly for this fishery, varies considerably through the season, as they grow faster in summer, and virtually cease growing in winter. Thus the numbers available for legal capture will depend on the month for each region and sex. It is known that the fishery follows these patterns to target the new recruits. By subdividing the population by length as well as age, seasonal patterns in exploitation can be modelled. Most importantly, the model-predicted numbers of catches-at-age to fit to otolith derived catches-at-age, and the predicted total catch by weight in each month, is more accurately described and thus the fits to these data sets more accurate.

In Chapter 11, the movement submodel was formulated using movement transition matrices. January, when migratory offshore or southward movement predominates, was chosen as the yearly time of model movement. This movement model was fitted to three decades of tag recoveries. The estimated movement matrices are incorporated in the estimator presented below. In each January time step they move fish from each cell to all others in proportion to rates estimated from the tag recovery data set.

The goal of work in this chapter was to incorporate these four basic inputs, (1) the monthly catch and effort data set, (2) the FRDC project catch-at-age samples, (3) the growth submodel, and (4) the movement submodel, into a single spatial and dynamic fishery model framework. This would allow the estimation of parameters which form the basis of an historical reconstruction of the South Australian King George whiting population over the months for which catch and effort data are available.

The following performance indicators will result as model estimation output: (1) yearly recruitment, (2) monthly exploitation rate, (3) monthly fishable biomass, (4) total fishable population numbers, (5) yearly egg production.

The model population variable array is a function of five independent variables, i.e. subdivides the population 5 ways: by (1) month, (2) spatial cell, (3) sex, (4) yearly cohort (i.e. age), and (5) for crossing cohorts, length slice.

12.2 Methods

King George Whiting Population Variable

The King George whiting model population variable array is written:

$$NKGW[it, icell, isex, icohort, islice] \quad (12.1)$$

where

- *it* = monthly time step. Model time runs over full financial years, starting from *it* = 1 in July 1976, and increases in monthly increments, to June 1998.
- *icell* = spatial model cell. There are 14 cells, described in Chapter 11.
- *isex* = female (*isex* = 0) and male (*isex* = 1).
- *icohort* = year class of King George whiting, assuming yearly cohorts, designated by the year each cohort was spawned. Spawning and thus birth date were defined to be May of each year (Chpt 4), with each cohort assigned an age of 1 month in that first May of spawning. For example, the cohort of fish spawned in May 1984 are designated by *icohort* = 1984. They enter the model population array, as yearly recruit numbers the following year, at age 13 months, in May 1985.
- *islice* = length subinterval, applied when the cohort is 'crossing' LML. Numbers in this slice are assigned as a proportion of the sublegal (< LML) lengths of the cohort entering the fishable stock in each monthly time step. Index *islice* from 1 to *nslice[icell, isex]* designates legal slices; *islice* = 0 refers to sublegals (Chpt 10).

Ages ran from 13 months (1 year) to 157+ months. The highest age is a 'plus' group, comprising fish of the oldest monthly age (12 years 12 months) and older.

Global Index Conversion Functions

A number of basic variables or indices of the model are not independent, notably those related to time. For instance, the model time step, *it*, is in months, with *it* = 1 being July 1976. It is often necessary to relate this model time-step index to calendar month number and year which data queries provide.

Similarly, the ages of fish in the model population array are given by the cohort year of their spawning (*icohort*), and the monthly time step (*it*). Frequently it was necessary to convert these two model population array subscripts into month of age which the growth description employs. Conversions of time indices were needed throughout the model code.

To carry out these transformations of the time and age variables, a number of 'index conversion functions' were defined and programmed as globally declared functions.

Two preliminary functions, the first standard in most mathematical programming languages, were employed in many of these function definitions. They are

1. A function that truncates all the decimal digits of any number, leaving only the integer, which we (following the Mathematica programming language) here denote "*IntegerPart*[any real number]".
2. We also employed a "Remainder" function that takes the remainder from any float or rational:

$$\text{Remainder}[x] := x - \text{IntegerPart}[x]$$

Three additional time indices were employed:

imonnum = calendar monthly name as a number, for example, for January, *imonnum* = 1.

iy = year of each data and model time step, e.g. *iy* = 1976.

iage = months of age starting at birth month, May of the spawning year of each cohort, *iage* = 1.

The global time index conversion functions, the indices converted, and their function definitions, are listed as follows.

1. *it* from *iy* and *imonnum*.

$$iFtYMn[iy, imonnum] = (iy - 1976) * 12 + (imonnum - 6)$$

2. *imonnum* from *it*.

$$iFmonnumT[it] = \text{Remainder}[(\text{Remainder}[it / 12] * 12 + 6) / 12] * 12$$

3. *iy* from *it*.

$$iFyrT[it] = (it + 6 - iFmonnumT[it]) / 12 + 1976$$

4. *iage* (in months, as always) from *it* and *icohort*.

$$iFageTCoh[it, icohort] = it - (icohort - 1976) * 12 + 2$$

5. *icohort* from *it* and *iage*.

$$iFcohortTA[it, iage] = (it + 2 - iage) / 12 + 1976$$

6. *imonnum* from *iage* (where, for example, *iage* = 1, 13, 25 etc. are May).

$$iFmonnumA[iage] = \text{Remainder}[(iage + 4) / 12] * 12$$

Index conversion functions were also written and used for converting among effort type indices and for mapping regions (Gulf St. Vincent, Spencer Gulf and West Coast) to the specific model spatial cells which comprise them. These functions have been tested against the full domain of inputs.

Effort and Catch Partition by Gear and Species Targeted

The effort variable was broken down by two levels of hierarchy. The top level is by sector: commercial and recreational. Recreational effort is a single effort type category. Commercial harvest was further broken down by 4 categories of gear type and 3 categories of target type. Commercial sector gear types are: (1) handline, (2) haulnet, (3) gillnet, (4) all other gear types (the latter yielding largely negligible catches for King George whiting). Commercial sector target types are: (1) specifically targeting King George whiting, (2) specifically targeting any other single species, (3) not specifically targeting any particular species.

From 1976/77 to 1982/83, the first seven years, species targeted was not recorded on the fisher catch log data forms. Thereafter target type was included. The effort type breakdown therefore differs for the two catch and effort time periods.

For the non-target early years, there are 5 effort types indexed by number, $i1Etype = 1$ to $n1Etype$: $i1Etype = 1, 2, 3$ & 4 are commercial harvest with $igear = 1, 2, 3$ & 4 , as enumerated above. $i1Etype = 5$ is recreational effort in this early “1” period.

In the subsequent “2” period, there are 13 effort types indexed by number, $i2Etype = 1$ to $n2Etype$, where $n2Etype = 13$:

- $iEtype = 1, 2$ & 3 are $igear = 1$ and $itarget = 1, 2$ & 3
- $iEtype = 4, 5$ & 6 are $igear = 2$ and $itarget = 1, 2$ & 3
- $iEtype = 7, 8$ & 9 are $igear = 3$ and $itarget = 1, 2$ & 3
- $iEtype = 10, 11$ & 12 are $igear = 4$ and $itarget = 1, 2$ & 3
- $iEtype = 13$ is recreational effort.

For example, $i2Etype = 4$, designates $igear = 2$, and $itarget = 1$, i.e. haulnet, specifically targeting King George whiting.

The model catch equation has the following form:

$$Cn[it, icell, isex, icohort, islice, iEtype] = q[imomnum, isex, iEtype] * NKGW[it, icell, isex, icohort, islice] * Effort[iEtype]$$

(12.2)

The catchability, q , was assumed to vary independently with month of the year, sex of the fish, and the effort type:

$$q[imonth, isex, iEtype] = qEt[iEtype] * sMn[imonth] * sSx[isex] \quad (12.3a)$$

Only one of the three factors in (12.3) serves as the overall catchability scaling factor, namely the component due to effort type. The selectivities for catch rate variation by month ($imonth$) and sex therefore vary above and below 1, and were defined relative to one arbitrarily chosen month and sex respectively: The selectivity by month, $sMn[imonth]$, was defined relative to January by setting $sMn[1] \equiv 1$ and the selectivity parameters freely estimated in other months, $sMn[2], sMn[3], \dots, sMn[12]$, where $imonth = 1$ is the monthly index for January.

For selectivity by sex, we set the coefficient for females, $sSx[0] \equiv 1$ where $isex = 0$ for females, and estimated $sSx[1]$.

Catchability coefficients for the early period were calculated as linear functions of the estimated catchabilities from the later period.

Specifically, we assumed a linear relationship between the $q1Et$ and $q2Et$, which allows only the same gear type to be related, specifically

$$\begin{aligned} q1Et[iEtype=1] &= a11 * q2Et[iEtype=1] + a12 * q2Et[iEtype=2] + a13 * q2Et[iEtype=3] \\ q1Et[iEtype=2] &= a21 * q2Et[iEtype=4] + a22 * q2Et[iEtype=5] + a23 * q2Et[iEtype=6] \\ q1Et[iEtype=3] &= a31 * q2Et[iEtype=7] + a32 * q2Et[iEtype=8] + a33 * q2Et[iEtype=9] \\ q1Et[iEtype=4] &= a31 * q2Et[iEtype=10] + a32 * q2Et[iEtype=11] + a33 * q2Et[iEtype=12]. \end{aligned} \quad (12.3b)$$

For the early years, we know (assume) that the sum of the catches from the different target types (which were not reported to us individually) equals the total catch that was reported. By setting the

So for the example of handline (HL) gear type we have

$$C1Et[iEtype=1] = C2Et[iEtype=1] + C2Et[iEtype=2] + C2Et[iEtype=3].$$

Substituting the form of catch Eqs. (12.2 & 12.3) for the early years, we find the a_{ij} 's are the proportions of effort in each target type, for any given gear type. For the HL example, we now have

$$\begin{aligned} a_{11} &= \text{Effort}[[i\text{Etype}=1]] / \text{Sum}[\text{Effort}[[i\text{Etype}=1]], \{i\text{Etype}=1,3\}] \\ a_{12} &= \text{Effort}[[i\text{Etype}=2]] / \text{Sum}[\text{Effort}[[i\text{Etype}=1]], \{i\text{Etype}=1,3\}] \\ a_{13} &= \text{Effort}[[i\text{Etype}=3]] / \text{Sum}[\text{Effort}[[i\text{Etype}=1]], \{i\text{Etype}=1,3\}] \end{aligned} \quad (12.3c)$$

and similarly for the other gear types.

Recreational catch and effort was measured in a two-year South Australian program that estimated catches and recreational boat hours using a boat ramp bus-route creel survey method, in 1994/95 and 1995/96 (Chpt 8). We combined these to get estimates of King George whiting catch by month and movecell, with some extrapolation needed in certain cells and months, notably on Kangaroo Island. Most recreational King George whiting catch is taken in small boats launched from public ramps. This yielded one full year of catch and effort totals. To extrapolate back and forward in time, we assumed recreational catch and effort varied over years in direct proportion to change in South Australian total population. Other plausible hypotheses for rates of change of recreational fishing can be tested to gauge the sensitivity to this data input. With recreational catch and effort making up about a third of the total, the lack of yearly information on changes in this component of the harvest remains the biggest information shortfall in the stock assessment of this resource.

Growth and Recruitment

The processes of growth and yearly recruitment were mediated by the slice growth submodel described in Chapter 10. The mean weight of each fish harvested, by monthly age and slice, were taken as inputs from the slice growth output files, considerably reducing computation during model estimation as noted in that chapter. A separate slice-growth input file was calculated for each combination of the 2 sexes, 3 regions (GSV, SG, WC), and 5 LML's (270, 280, 290, 300, 310).

Model catch totals by weight were converted from model numbers captured (Eq. 12.2) by multiplying the corresponding slice- and age-specific weight, and adding to the catch total.

Yearly recruit numbers in every spatial cell and for each yearly cohort were independently estimated parameters. Recruits were added to the population in May of each year at age 13 months. Legal size fish enter the fishable stock monthly as a newly created slice. Slices were used to subdivide only the legal component of the 'crossing' cohorts, as noted. The new legal slice was calculated each model month as a proportion of remaining sublegals in the crossing cohort (tabulated as *Psublegslice*, Table 10.3 for the example of GSV females LML = 280 mm in Chapter 10).

As noted in the Introduction and in Chapter 10, only the 'crossing' cohort ages were subdivided by length into slices. Thus, there were three basic categories of cohort in this model description:

1. Sublegals. These denote cohorts all of which were smaller in length than LML. In practice, this designation was made by defining a cohort as sublegal if 2% or less of its normal length-at-age distribution fell below LML.
2. Crossing cohorts. Those ages for which the fitted normal length-at-age distribution straddles LML.
3. Postlegals. Cohort ages which lie (>98%) above LML, so that nearly all the fish of these ages are large enough for legal harvest.

The ages that separate these three categories depend on growth, i.e. the mean and standard deviation of the length-at-age distributions estimated in Chapter 9, and thus will vary with the two sexes and three regions.

Natural Mortality

Natural mortality is modelled in a standard manner (Hilborn and Walters, 1992) as a uniform monthly multiplicative survival factor, $e^{-M/12}$, on all elements of the fish population array.

The estimate of $M = 0.55$ was obtained from three methods of estimation. By Jones et al. (1990) using the Pauly methods based on biological characters of the species, (1) growth constant, K , and water temperature, and (2) using the maximum observed age of the fish.

Under the current project, a third estimate of M was obtained from population measurements (3) using a regression analysis of total mortality, Z , versus effort, in the manner of Garrod (1967). Writing $Z = F + M = qE + M$ and regressing Z versus E for each available time period and area of the South Australian King George whiting fishery yielded an estimate of M as the y-intercept and q as the slope. The Z 's employed were estimated from tag recoveries as the reciprocal of mean time-at-large (Gulland 1955; Chapman 1961).

Though they were all characterised by relatively wide confidence bounds, the three methods roughly agreed, yielding this relatively high estimate of natural mortality rate.

Movement

Movement transition matrices were multiplied by the vector of numbers in each spatial cell at the beginning of each January time step, yielding numbers in the post-movement cells. The matrices for *P1* and *P2*, whose derivations were presented in Chapter 11, apply to 33-month-old and 45-month-old fish respectively. The *P2* matrix, estimated for tagged fish of age 45 months in January of their time at large, was also applied to move all older aged King George whiting.

In West Coast cells, the destination of migratory fish remains uncertain. No fish from West Coast commercial harvest samples showed evidence of spawning. Also, all of such samples were largely based on fish that were aged 3 years or less. Thus, the fishery on the West Coast did not overlap with spawning aggregations and tag recaptures did not indicate rates of movement to the (hypothesised offshore) spawning locations. Fishing on the West Coast occurs in inshore bays where King George whiting abundances are high and costs of fishing low. Searches were carried out further off-shore by SARDI researchers aboard the RV *Ngerin* at the anticipated time of spawning (from the otolith microstructure of post-larvae) but no success was achieved in finding offshore spawners.

Thus, since few fish above the age of 3 are captured, we know that they do migrate from the inshore bays. However, we do not know where they end up. Thus, unlike Gulf St. Vincent and Spencer Gulf where spawning aggregations are known (Chpt 3), for the West Coast we can only hypothesise their existence. Consequently, a 14th spatial cell was defined as the hypothetical destination of West Coast migration. Because no tags were recovered from this cell, rates of migration must be inferred from the absence of older fish in commercial (and recreational) catch.

To this end, three additional estimated parameters were added to the migration rate probability matrices, allowing movement to cell 14. In model fits to catches and catches-at-age when rates of fishing mortality are insufficient to explain low levels of ages 4+ in the catch, the model will achieve better fit by allowing these offshore migration rate parameters (to cell 14) to increase.

Parameters

Parameters for the model fall into six general categories: (1) annual recruitment numbers for each model spatial cell; (2) catchabilities; (3) month selectivity (4) sex ratio selectivity; (5) likelihood standard deviations (sigmas) for the catches by weight, by spatial cell and effort type; (6) added movement rate parameters to hypothesised spawning area off the West Coast.

Effort is throughout taken as an input directly from data (i.e. the model is conditioned on effort).

Initialisation: State Array and Parameters

The initial population state variable array and the initial parameters were obtained using a two-stage method. First, the initial population state array ($NKGW0$) was derived assuming a steady-state age structure. In the second stage, initial parameter estimates were inferred from the population array, in combination with catch and effort data. Total mortalities by spatial cell, derived from tag recoveries as noted above, were also basic inputs. We sought the initial state array for the end of June, 1976, immediately prior to the first month of data, which was also the beginning of the monthly time step iteration of the dynamic model.

For initialisation, no movement was considered, rather, each cell's initial recruitment and catchability was derived independently of other cells. Sex ratios in all cells were assumed to be 50:50, however, the initial population array for each sex was estimated independently since the slice growth breakdowns are sex-specific.

Steady-state recruitment numbers in each cell were the quantities to be derived. Taking these as unknown variables, the numbers in each cohort (and, for crossing cohorts, in each slice) above recruitment were inferred from the tag-derived estimates of Z by cell, assuming a steady-state age structure. These depend on the number of months each age/slice was in the fishery subsequent to recruitment, and how many months subject only to natural mortality. This yielded a full population array once absolute mean recruit numbers were estimated.

The inputs from the slice growth description were:

- $P_{slice}[iregion, isex, iage]$
- $P_{sublegslice}[iregion, isex, iage]$
- $cohortWt[iregion, isex, iage]$
- $sliceWt[iregion, isex, iage, islice]$,

the definitions of which were presented in Chapter 10.

The initial recruitment variables to be solved in each cell were denoted $R0[icell]$. Since the first monthly age accounted for in the model population variable is month 13, which occurs at the beginning of the May time step, this is the age of $R0$. Subsequent survival was calculated in two parts: (1) over the first two months May and June, from time of recruitment to the time we seek for the initial array, end of June, giving the predicted survival from $R0$ to the youngest cohort in the initial population array; (2) yearly survival to subsequent yearly higher ages of the initial population array.

The survival rate over these time intervals is due to natural mortality below LML and due to both natural and fishing mortality above LML. Total survival factors to the June 1976 age and, for June crossing cohorts, slices were calculated using monthly and yearly rates of $\exp[-M/12]$ and $\exp[-M]$ for natural survival, and $\exp[-Z[icell]/12]$ and $\exp[-Z[icell]]$ for total survival where $Z[icell] = M + F[icell]$. Only fishing mortality varied with spatial cell.

For sublegal cohorts, the survival factor was

$$S_{sub}[icell, isex, icohort] = \exp[-M/12]^2 * \exp[-M]^{(cohort1 - icohort)}, \quad (12.4a)$$

where *cohort1* designates the cohort birth year of the youngest age in the initial (June 1976) population array.

For crossing cohort and slice, the survival factor was

$$S_{cross}[icell, isex, icohort, islice] = \exp[-M/12]^2 * \exp[-M]^{(cohort1 - icohort)} * ((\exp[-Z[icell]/12])^{(imonleg0[icell, isex, icohort] - islice + 1)}), \quad (12.4b)$$

where *imonleg0[icell, isex, icohort]* designated the first month that the slice in question became subject to harvest.

For postlegal ages, the survival factor was

$$S_{post}[icell, isex, icohort] = \exp[-M/12]^2 * \exp[-M]^{(cohort1 - icohort)} * ((\exp[-Z[icell]/12])^{((agesliceUB[iregion, isex] - agesliceI[iregion, isex] + 1)/2)}) * ((\exp[-Z[icell]/12])^{(ageLastPostlegCoh - agesliceUB[iregion, isex] + 1)}) * ((\exp[-Z[icell]])^{(cohortPostleg100[icell, isex] - icohort)}), \quad (12.4c)$$

where *agesliceI[iregion0, isex]* and *agesliceUB[iregion, isex]* designated the first and last month when the cohort was crossing, *ageLastPostlegCoh* is the last month of age of the first postlegal cohort, and *cohortPostleg100[icell, isex]* is the cohort birth year of the last Postlegal cohort.

The factor $((\exp[-Z[icell]/12])^{((agesliceUB[iregion, isex] - agesliceI[iregion, isex] + 1)/2)})$ is survival rate over all legal-size crossing months assuming approximately that an average fish in the crossing cohort spent a number of months in the fishery equal to about half the total number of slices. $((\exp[-Z[icell]/12])^{(ageLastPostlegCoh - agesliceUB[iregion, isex] + 1)})$ is the predicted survival

over the months of the postlegal cohort to the end of the following June, in the year when the cohort first becomes postlegal. $((\exp[-Z[icell]])^{(cohortPostleg100[icell, isex] - icohort)})$ is survival over all subsequent postlegal years.

Recruit numbers were solved for by a single equation in each spatial cell, setting the sum of fishable biomass times monthly exploitation rate equal to reported mean monthly catch. These recruitments for each cell were then used to infer the population numbers for each age and slice, from the same set of steady state survival factors subsequent to recruitment at age 13 months.

Likelihood

The likelihood function has three components for fitting to the three data sets: (1) catch totals by weight in each cell and monthly time step; (2) proportions of catch-at-age in numbers, available for selected months and cells during the current FRDC program, 1996 to 1998; (3) the sex ratios in each monthly catch-at-age sample. An additional likelihood term for the sex ratio estimate (a single parameter of sex catch selectivity) was needed, even though it uses the same data sets as (2) because the model predicted catch proportions by age are fitted independently to data sets for males and females in each cell and month sample. So (2) provides no information about the relative numbers of males and females.

Catches-by-weight

For fitting to monthly catch totals, the normal likelihood, L , for each choice of cell, $icell$, and effort type, $iE2type$, was written:

$$L_{Cw} = \prod_{icell=1}^{13} \prod_{iE2type=1}^{nE2type} \prod_{it=1}^{ntest} \frac{\exp\left[-\frac{1}{2} \left(\frac{C[it, icell, iE2type] - \hat{C}[it, icell, iE2type]}{\bar{C}[icell, iE2type] \cdot \sigma^c[icell, iE2type]} \right)^2\right]}{\sqrt{2\pi} \sigma^c[icell, iE2type]} \quad (12.5)$$

where

it = the model time step running from 1 to $ntest$;

$\sigma^c[icell, iE2type]$ = the estimated standard deviation parameter for each cell, $icell$, and effort type, $iE2type$;

$C[it, icell, iE2type]$ = the reported catch by weight total for each time step, it , cell, $icell$, and effort type, $iE2type$;

$\hat{C}[it, icell, iE2type]$ = the predicted catch by weight total for each time step, it , cell, $icell$, and effort type, $iE2type$;

$\bar{C}[icell, iE2type]$ = the reported mean catch by weight total averaged over time step for cell, $icell$, and effort type, $iE2type$.

Because catches-at-age were only available for the second time period of catch and effort data when species targeted was recorded, catchabilities for the early period, which rely on catches-at-age, via mortality, could not be estimated. Therefore we could not fit to catch and effort totals in the early (June 76-June 83) period. The fits of Eq. (12.5) were applied only to the second (July 83+) catches, over the $iE2type$ index where target type is explicit. Catchabilities for the early period were calculated from the estimated values of the later period from Eqs. (12.3b and 12.3c).

The inclusion of the mean catch, $\bar{C}[icell, iE2type]$, effectively as a scaling factor on the estimated standard deviation, was done to allow easy estimation of the initial values for the $\sigma_{m, iE}^C$ array, taken as 0.25, since in this form, $\sigma_{m, iE}^C$ is approximately equal to the coefficient of variation.

Catches-at-age

For catch-at-age samples a multinomial likelihood was employed. Because the multinomial distribution is defined uniquely by the predicted set of probabilities, no additional standard deviation parameters are estimated for this likelihood component. Furthermore, since we are fitting to a finite probability mass function (pmf, i.e. a discrete set of probabilities, each as the proportion of the catch in each age, with the range of ages being bounded from 1 to the 12+ age class) for each catch-at-age sample, a multinomial is a natural distribution choice.

For the observed data, proportions are not required, rather the multinomial likelihood is formed using the raw observed numbers-at-age.

One additional advantage of the multinomial in likelihood formulation, where a number of separate samples are fitted, is that the weighting of each particular age sample term in the log-likelihood sum is directly proportional to the sample size.

The overall multinomial was written

$$L_{CnA} = \prod_{itCnA=1}^{nCnA} \prod_{iage=1}^{12} (\hat{P}[itCnA, iage])^{nCnA[itCnA, iage]} \quad (12.6)$$

where

$itCnA$ = index over the full set of $nCnA$ catch-at-age samples;

$\hat{P}[itCnA, iage]$ = model predicted proportions captured by age, for each sampled month and cell, indexed by $itCnA$;

$nCnA[itCnA, iage]$ = observed fish numbers in each age, obtained from catch-at-age sample $itCnA$.

Sex ratios

Because all data was fishery derived, only sex ratios in the catch are known. Any observed differences in the sex-specific numbers captured may result from differences in either (1) numbers in the population, or (2) the selectivity of the gear.

To determine whether any deviation from 50:50 sex ratio is inherent in the population prior to reaching harvestable size, i.e. in recruitment, research small-mesh beach seine samples of largely 1-year-old fish were examined. These King George whiting were gathered in the current state-licence-fee sponsored yellowfin whiting program. Though there was substantial variation from 50:50 in individual samples, no significant overall difference in numbers of males versus females was observed. Thus, any deviations from even sex ratio in the catch-at-age samples will be assumed to reflect sex-specific differences in gear selectivity.

As noted, with female selectivity assigned the value of $sSx[0] = 1$, the relative sex selectivity parameter is that for males, $sSx[1]$, in Eq. 12.3. A single sex selectivity parameter was employed for all spatial cells.

Like catches-at-age, the proportions of male and female sum to 1 and thereby form a finite pmf of two possible outcomes. The binomial likelihood distribution was therefore employed.

The binomial sex-ratio likelihood component was written

$$L_{SexRatio} = \prod_{itCnA=1}^{nCnA} \prod_{isex=0}^1 (\hat{P}[itCnA, isex])^{nCnSex[itCnA, isex]} \quad (12.7)$$

where

$\hat{P}[itCnA, isex]$ = model predicted proportions of females ($isex = 0$) and males ($isex = 1$), from catch samples by month and cell, indexed by $itCnA$;

$nCnSex[itCnA, isex]$ = observed fish numbers in each sex, for each catch-at-age sample, $itCnA$.

Objective Function Minimisation

The negative logs of likelihood components were summed to form the model objective function.

Penalty functions were also added to the objective function to ensure that catches could never exceed existing population numbers in each cell and time step, and for each population subcomponent, sex and cohort or slice.

The objective function was minimised using the AD Model Builder model parameter estimation software. This package uses a powerful algorithm for calculating derivatives, reverse auto-differentiation, that allows model solution convergence in computation times one or several orders of magnitude faster than conventional minimisation methods. Even with the use of auto-differentiation, the King George whiting model, with 501 parameters, required several days of computation time to achieve a good level of minimization.

As with all likelihood estimation using multiple data sets, the weighting of different likelihood components remains a choice of the modeller. In results presented below the following likelihood weights were applied: catches-by-weight 1, catches-by-age 0.5, catch-sex-ratio 1.5.

12.3 Results

The resulting fits to the two principal data sources, catches-by-weight (Fig. 12.1-12.3) and sampled catch numbers-at-age (Fig. 12.4-12.5), plus recruitment timeseries, are plotted.

The fits to catches-at-age are less precise. These reflect the relative weightings assigned. The catch-at-age samples, are characterised by relatively higher levels of sample variation, and thus overall error, than the catch totals. Thus the closer fits to catch totals by weight are appropriate, catches totals providing more precise information about the population.

Two- and three-year old cohorts strongly dominate in nearly all spatial cells except for the two known locations of spawning aggregations, cells 7 (GSV) and 5 (SG) (Chapter 13, Figure 13.1).

Recruitment timeseries within each region exhibit a relationship between migratory 'sink' spatial cells and migratory 'source' spatial cells. The level of recruitment is noticeably low in spatial cells that experience relatively high levels of immigration and low levels of emmigration, compared to spatial cells with the opposite migratory characteristics. The estimation program has been run without the migration component which resulted in the recruitment timeseries showing no source-sink segregation of recruitment levels.

The estimate for male selectivity equals 0.80, suggesting either fewer males exist in the population, or else that fewer males get caught.

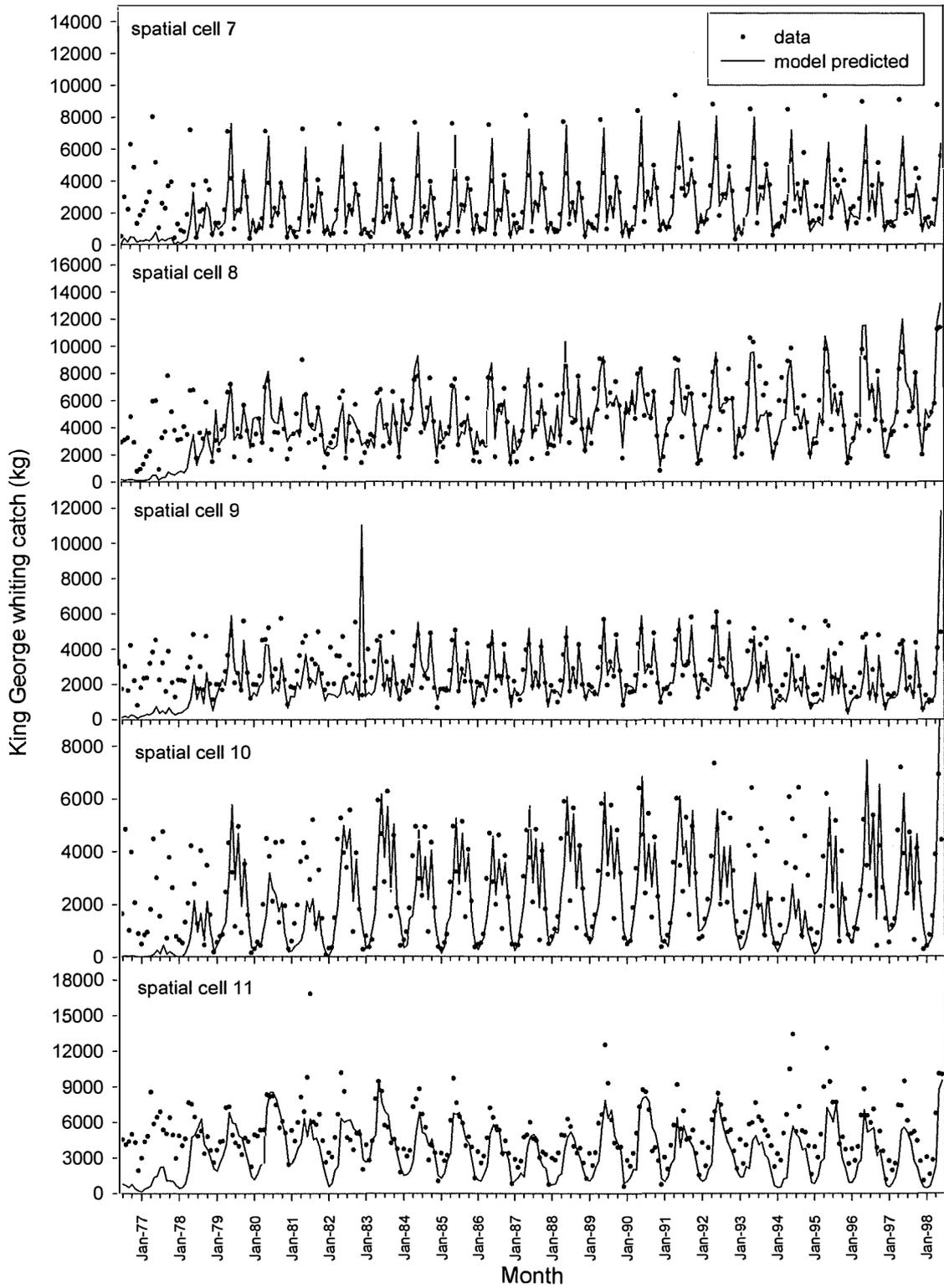


Fig. 12.1. Monthly reported (dots) and model predicted (line) catch totals by weight for the five spatial cells in the Gulf St Vincent region.

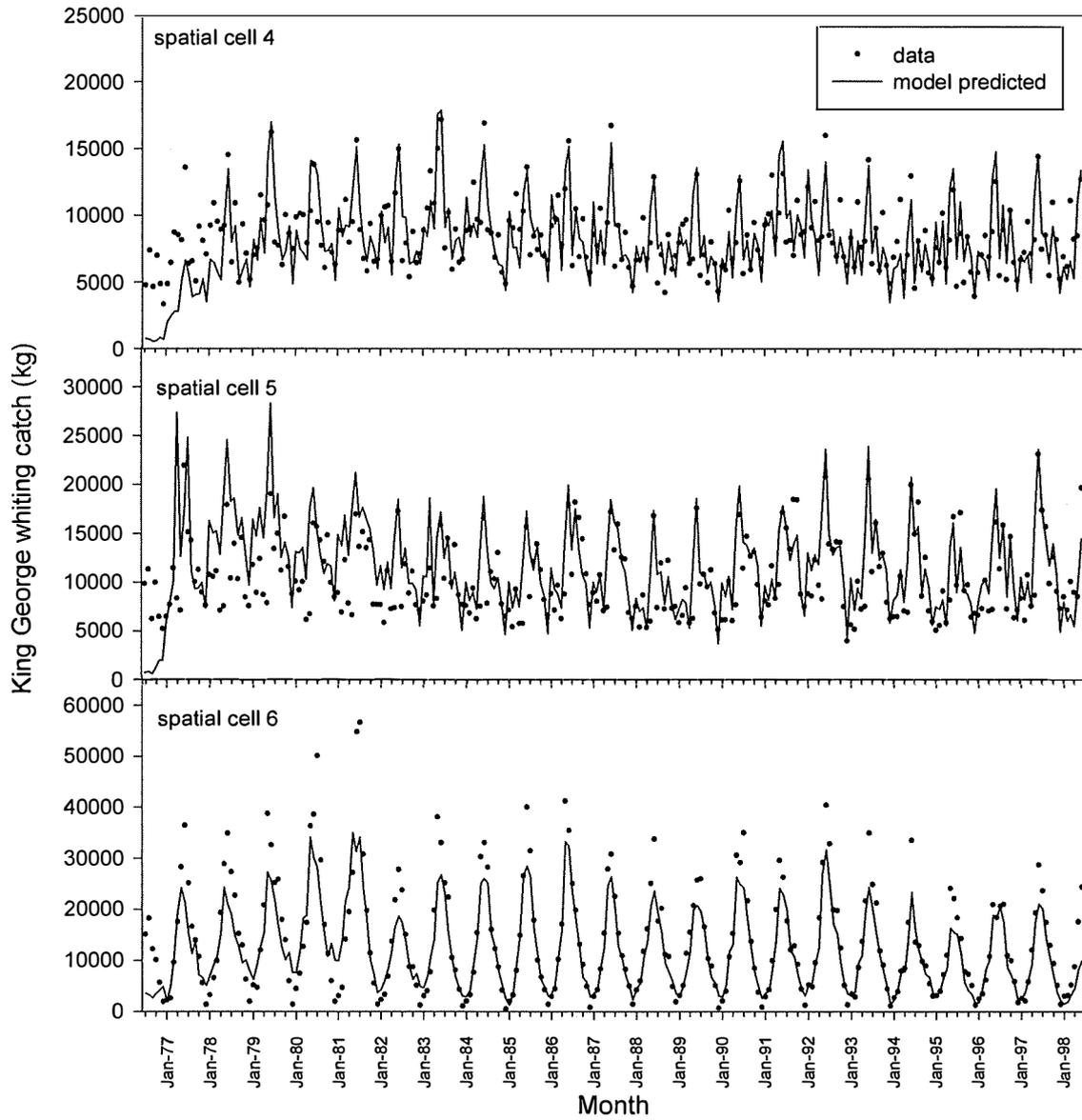


Fig. 12.2. Monthly reported (dots) and model predicted (line) catch totals by weight for the three spatial cells in the Spencer Gulf region.

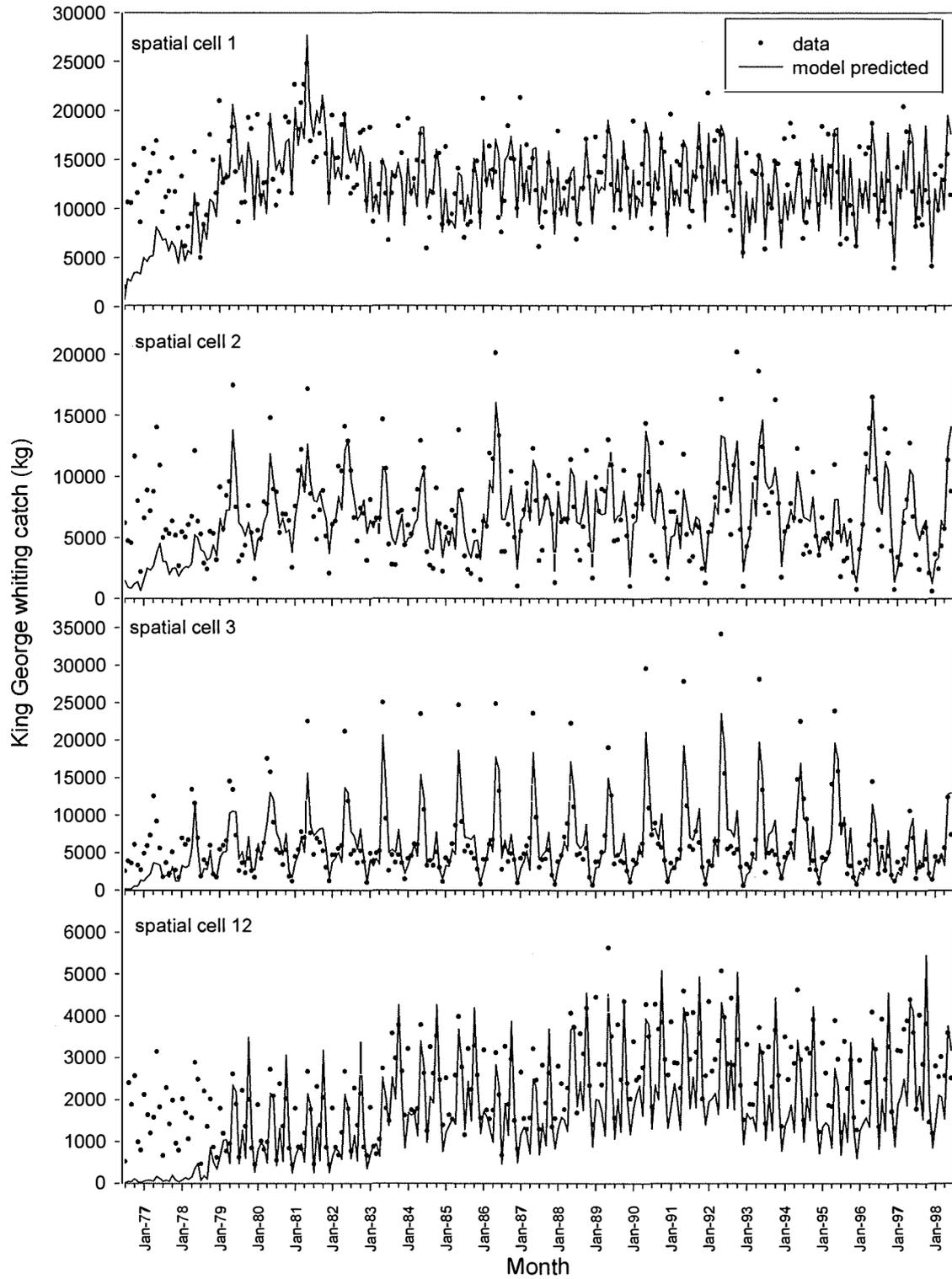


Fig. 12.3. Monthly reported (dots) and model predicted (line) catch totals by weight for the four spatial cells on the West Coast.

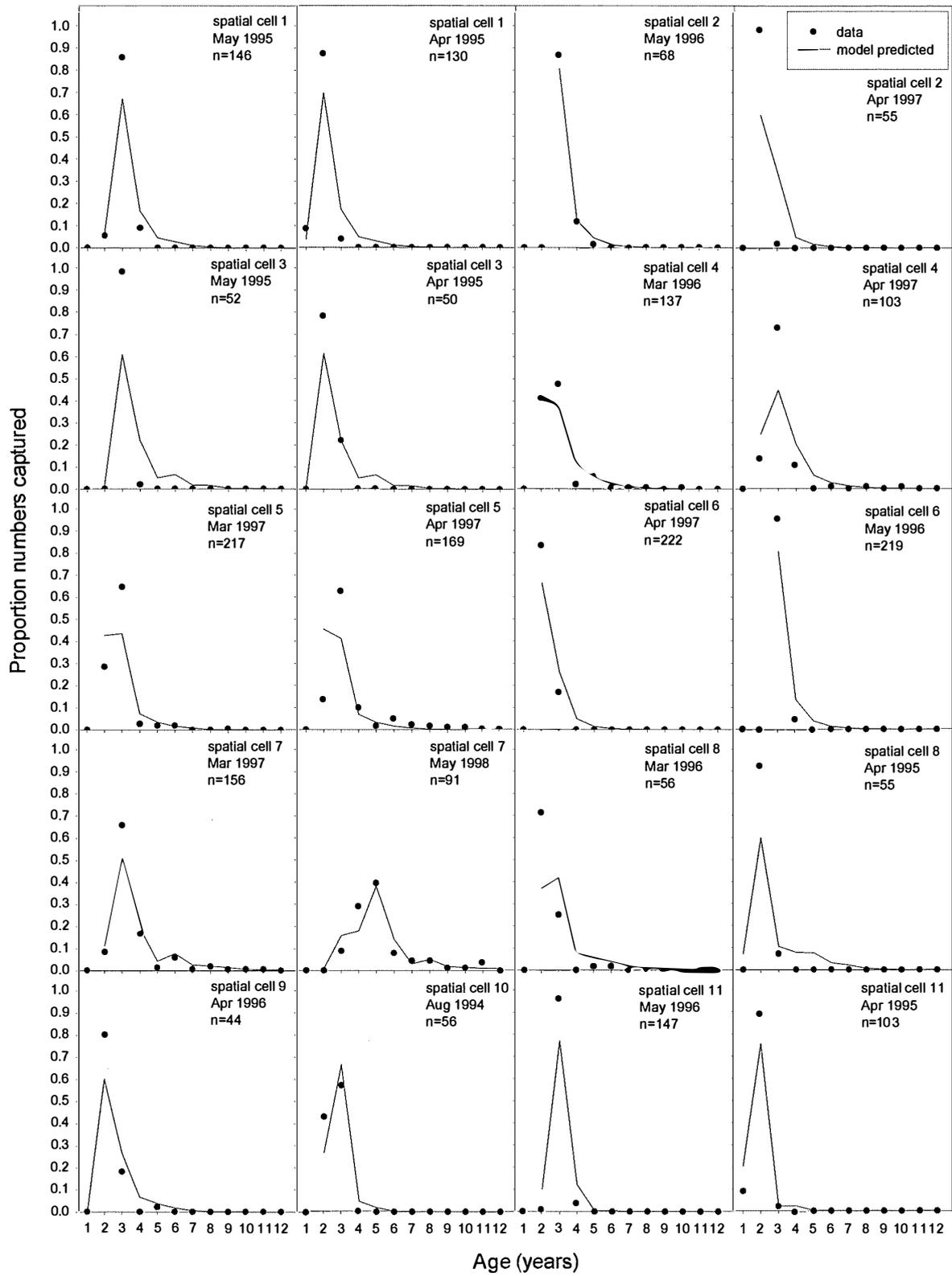


Fig. 12.4. Legal-sized female catch-at-age samples, model predicted (line) and observed (dots).

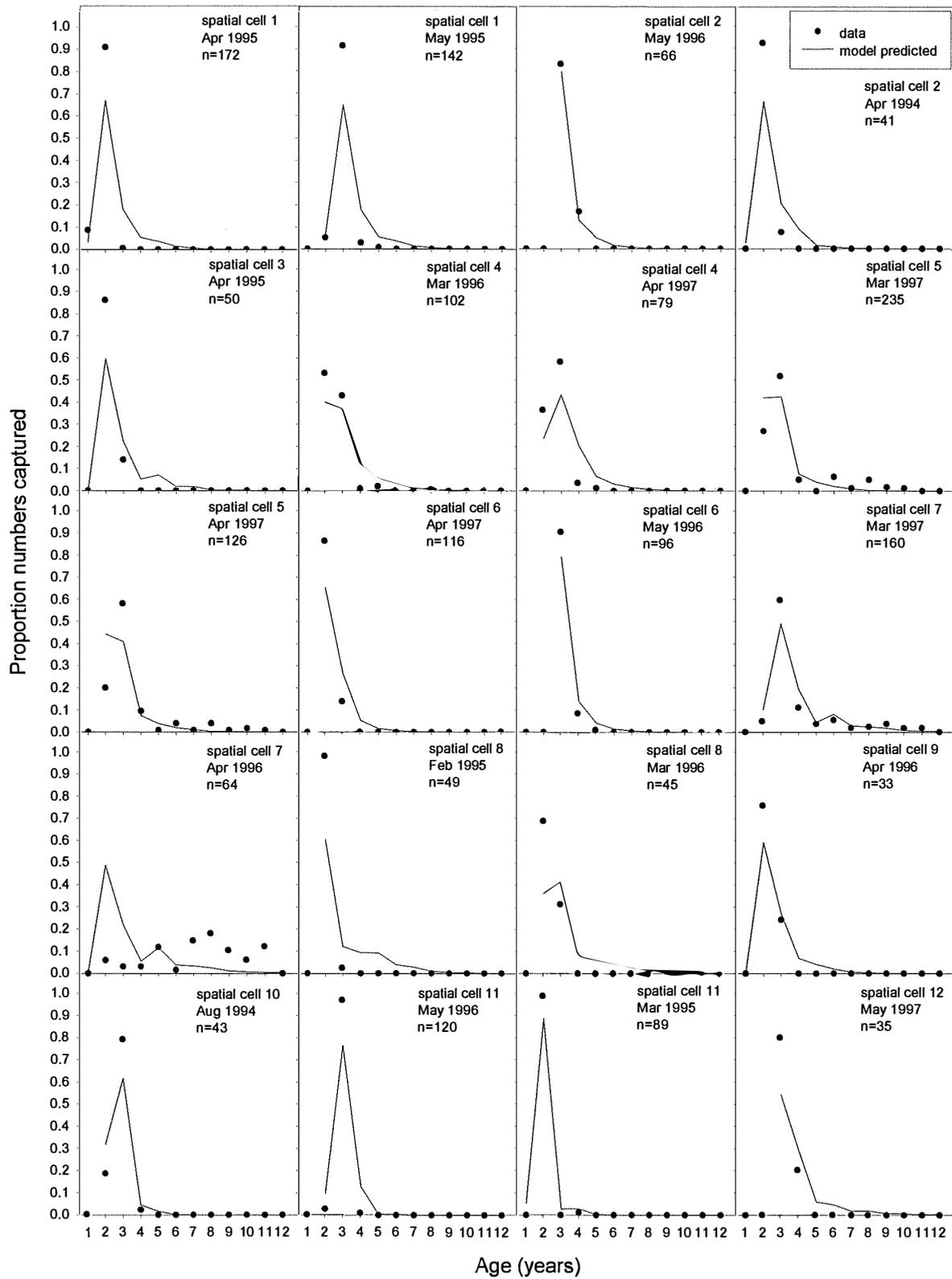


Figure 12.5. Legal-sized male catch-at-age samples, model predicted (line) and observed (dots)

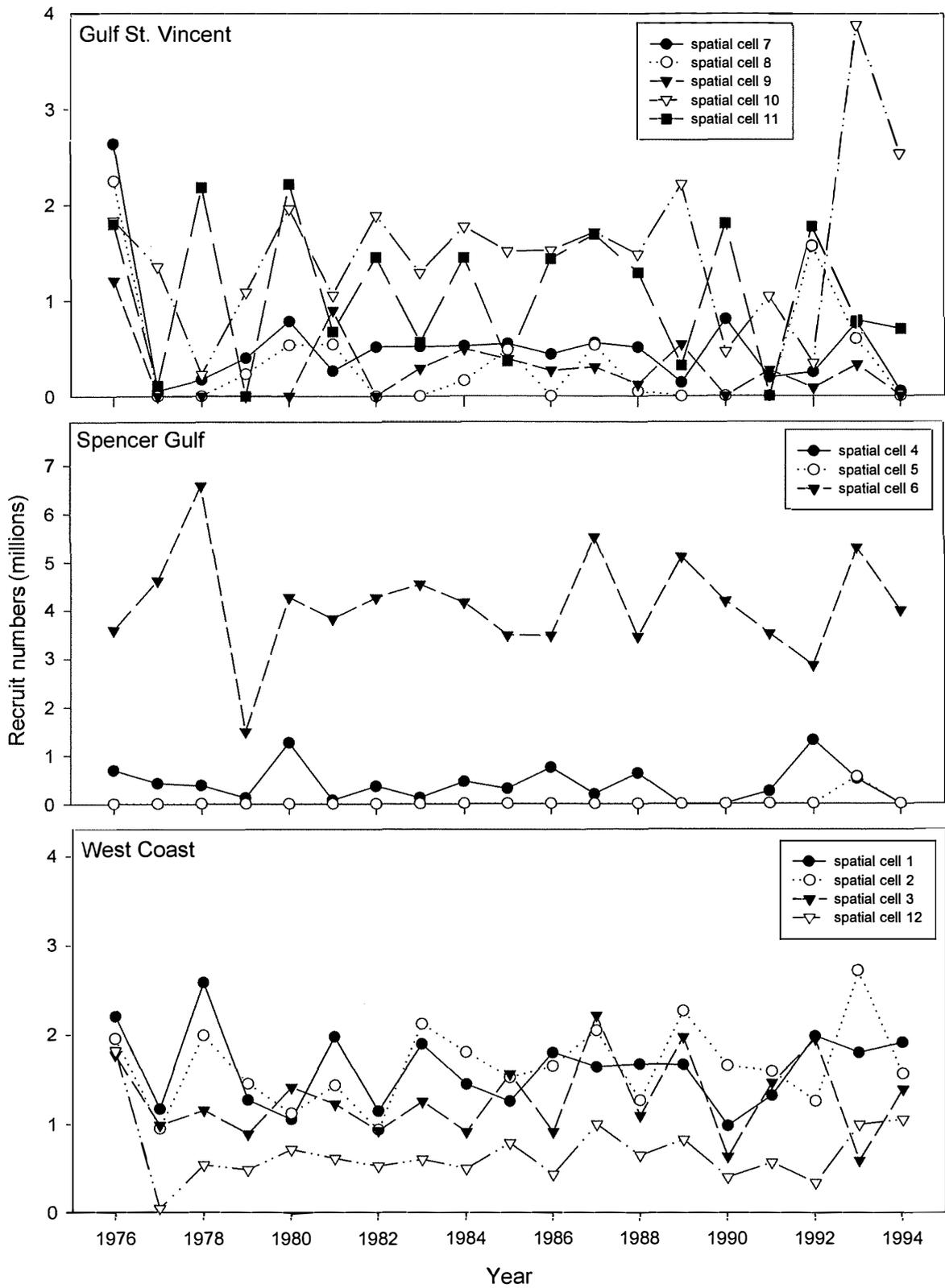


Fig. 12.6 Estimated recruitment time series for each of the three geographic regions.

12.4 Discussion

Modelling the South Australian King George whiting fishery posed two principal challenges:

- (1) the levels of exploitation of this stock are unusually high in the first year of adult (harvestable-size) life. In spawning aggregations, levels of exploitation are lower. Model spatial cells were chosen to separate these subpopulations.
- (2) The life history is characterised by high rates of early adult movement. Thus the spatial dynamics are reflected in the levels of fishing and the locations of fish of different age. Selectivity changes with age were assumed to be associated with the movement to areas of lower exploitation.

As noted in the Introduction, to represent this complex population dynamics, an unusually rich spatially-resolved data set was available.

South Australian commercial fishers have reported catch and effort by species targeted, in addition to gear type, since 1983. The rich breakdown of effort in this multi-species, multi-gear fishery, enhanced the information content of the catch log data set, in particular allowing the partition of catchability into the constituent components, thereby improving the accuracy of catch and effort data as a measure of stock abundance.

The most important data source, in addition to catch and effort data, were catch-at-age samples. 10781 fish were gathered in the current FRDC program. These yielded the detailed length and age based description of the growth of each cohort, analysed in Chapters 9 and 10. Information about relative numbers in successive ages also resulted from this data source providing reasonably good information about mortality. In addition, from this same data source sex selectivity information was obtained, enabling sex to be an attribute of the model population.

The movement of King George whiting was quantified by analysis of the extensive tag recovery data set. Though the tag-release numbers and locations were diverse in time and space, occurring over three decades from the mid 1960's to the late 1980's, the picture over that time was consistent, and the movement rates were consistent with the life history inferred from the catches-at-age, and from visual maps of movement direction trends.

Tag recovery data was also used to obtain preliminary estimates of total mortality in each cell, using the reciprocal of mean time at large. This permitted the steady state construction of an initial population array and initial parameter values.

The model presented above incorporates a more detailed description than conventional age-based approaches in three ways:

- (1) The time step is monthly, so that monthly variation in both the catches at age and in the catch totals are reflected in model output.
- (2) The movement of fish among cells is explicit.
- (3) The population array is broken down by length, in addition to age.

The monthly rather than yearly time step offers two advantages, besides the obvious one that the data sets themselves are monthly.

- (1) The seasonality of this fishery is relatively strong. Recruits are targeted in winter following growth to legal size in late summer and autumn. The variation in catch and catchability by month, along with the monthly growth of the cohort length-at-age distribution allow this seasonality to be represented.
- (2) The short time, generally less than a year, that fish in this population survive once reaching harvestable size, together with strong movement away from upper Gulf fishing grounds after about a year or less, means that the usual method of estimating mortality, by comparing abundance of cohort numbers over successive yearly ages, is not applicable. Instead the monthly change in both catch totals by weight, and in the catch numbers with age, allow inference about mortality from monthly change in population structure. Monthly catches-at-age allow inference, just as they do with fisheries depleted over yearly time scales, by the rate of depletion of age classes, principally the newly recruited one, through time. Catches-by-weight contribute information reflected in the overall rate of depletion of the yearly recruited stock, reflected in monthly changes in CPUE. In this fishery, monthly change in total catch provides additional information about mortality, because the overall catch is largely from just the one (or, in low catch months of summer, at most two) newly recruited cohort(s). It is for this reason that knowing the monthly growth of new and surviving biomass to the fishable stock is of particular value in this high mortality fishery model.

The fitting to the detailed breakdown of effort by gear and target type, provides an implicit method of non-linear effort standardisation. The catchabilities are estimated for each combination of gear and target, thus avoiding any potential problems with under-described covariances between these two forms of effort type which might occur if the catchabilities due to gear and target were assumed to vary independently.

Generally, the fits to catch totals and catches-at-age are qualitatively good, reflecting a relatively accurate characterisation of the spatial population dynamics. The results were shown in various model formulations, to be sensitive to the movement dynamics, in particular since the absence of year

classes of various ages in the catches-at-age may be due to either depletion by fishing or movement, in particular away from the upper Gulf cells. In addition, we found that the predicted recruitment series were also sensitive to the relative likelihood weightings of catches-at-age versus catches-by weight.

12.5 References

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CHAPTER 13. SOUTH AUSTRALIAN KING GEORGE WHITING MANAGEMENT MODEL: SIMULATOR

P. Gaertner

13.1 Introduction

The King George Whiting Simulator (WhitSim) is a simulation version of the Whiting Estimator (WhitEst) (Chpt 12) encased inside a graphical user interface (GUI) that includes geographical information systems (GIS). WhitSim provides the ability to simulate various management strategies and parameter scenarios and interrogate results of the simulation via in-built statistical, curve fitting and indicator analysis modules.

The model recreates changes in the whiting population under the different levels of fishing and fishing regulations within the 58 South Australian Marine Fishing Areas. WhitSim however, doesn't simulate the population within these fishing areas, but collates the fishing areas into the 13 "Movecells" (Chpt 2) (Fig. 13.1). The Movecells constitute three regions; West Coast, Spencer Gulf and St. Vincent Gulf.

The package is developed in the Borland Delphi programming environment and uses Paradox 5.0 databases to hold the default parameter and strategy information. Project files are used to store data from simulated management strategies and parameters, together with all output data from model. These projects are stored in the model subdirectory. A default project and a baseline project are included in the software distribution that contains data and parameter values extracted from the Whiting Estimator. The baseline project is automatically loaded with the model when WhitSim is executed. Although users are able to redefine the baseline parameters by saving a new baseline, the default cannot be altered.

13.2 Simulator Architecture

Fig. 13.2 schematically illustrates the WhitSim architecture. The architecture has four primary and two secondary components. The primary components include input and data manipulation modules, a strategy and regulation modules, the simulator and the analysis and statistical toolboxes. The secondary components include the external databases and information systems. Fig. 13.2 illustrates the interactions between system components.

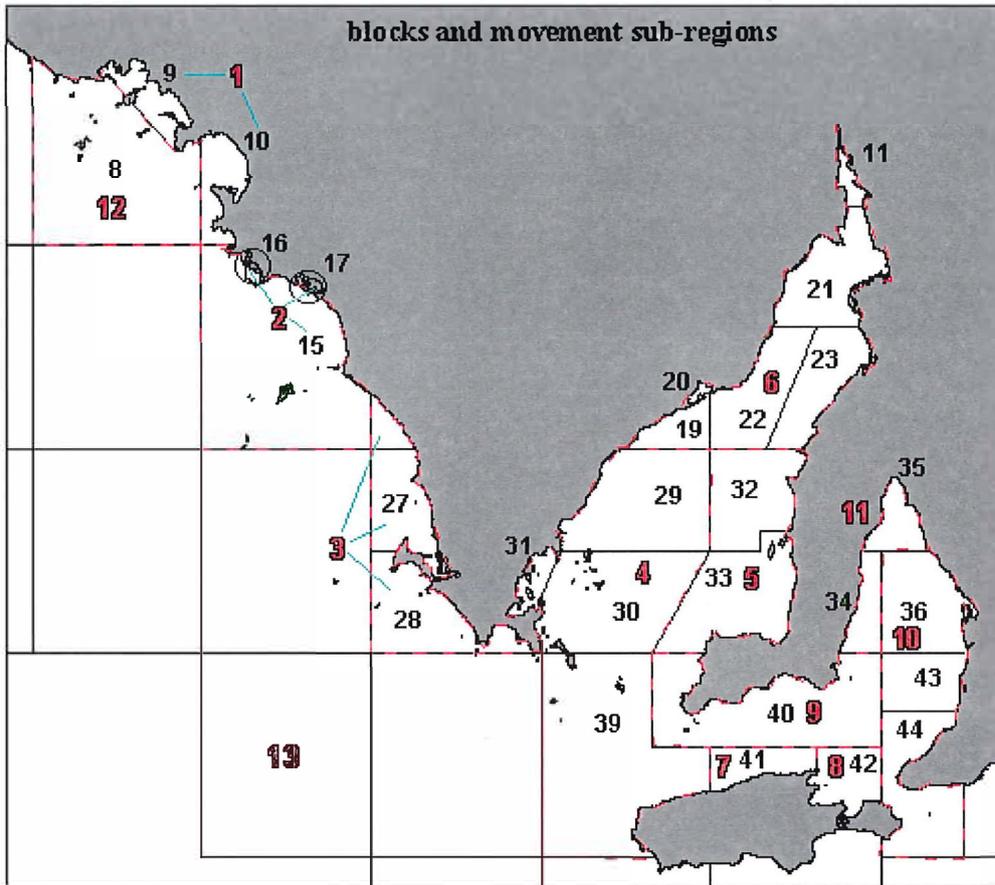


Fig 13.1 Map of South Australia showing the Marine Fishing Areas (black numbers), and the 13 Movecells used in the simulation model.

As mentioned above the databases are designed using Paradox 5.0 and act to provide parameter data for the WhitSim primary model input components. These databases are somewhat hidden from the users, and although users can alter them using an appropriate interface, it is not recommended and may cause the package to not operate correctly. Within WhitSim users alter the database variables by creating new project files.

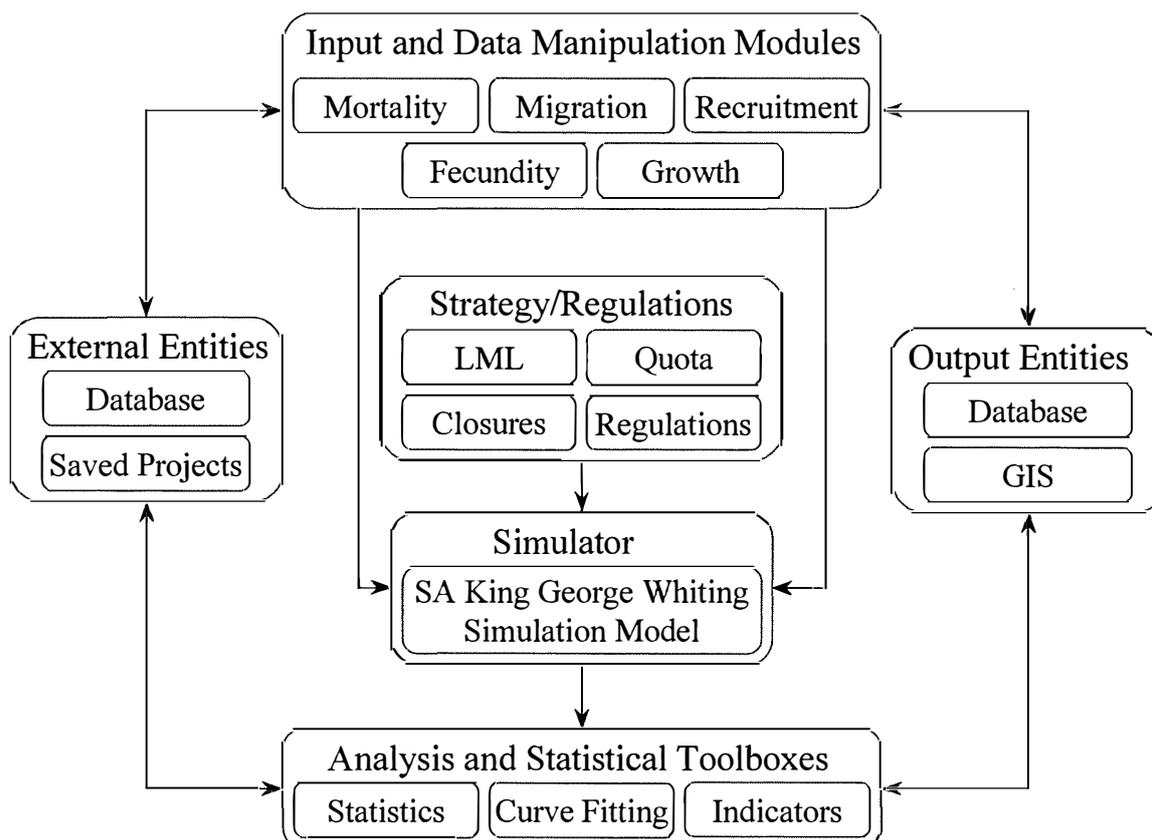


Fig. 13.1 WhitSim Architecture

13.3 WhitSim Command Structure

The WhitSim command structure is based around the four primary architectural components. Table 13.1 describes the functionality of the system.

Table 13.1 WhitSim Functionality

File	Open and save model projects, generate text summaries, simulation reports, and exportation of data to Excel, Word etc. Speed buttons are provided allowing the execution of the most widely used of these commands.
Parameters	Change mortality, migration and recruitment parameters for simulations.
Strategy	Specify the management strategy and fishing regulations.
Simulate	Execute the model.
Results	Display the model output and interrogate model variables via the GIS.
Analysis	Perform statistical; curve fitting and indicator analysis.
Window	Control display windows.

Table 13.2 describes the sub-menu functionality.

Table 13.2 WhitSim Menu Commands

File	New Project	Creates an empty project file and resets all parameter and strategy variables back to their baseline values.
	Open Project	Open an existing “saved” project file. Only project files created by WhitSim should be opened. If non-project files are selected the system may not operate correctly.
	Save Project	Projects can be saved at any time. However, it is recommended that projects be saved after the simulation model has been executed. To accomplish this, WhitSim will prompt users to save their projects at the completion of simulation.
	Save As	Allows projects to be renamed within the system.
	Load Baseline	The baseline scenario is the model’s reconstruction of the history of the fishery and contains the parameter values found in the whiting estimator. Although, the baseline project is automatically loaded when the package initialises it can be reloaded at anytime using this function.
	Save As Baseline	It is not anticipated that users will need to alter the baseline parameters. However, users may, if they choose, create a new baseline scenario based on a different set of parameter values.
	Reset Baseline	Restores the default baseline parameters kept within the system.
	Printer Setup	Allows the setup of local printing devices for use in the package.
	Export Data	Allows parameter and simulation data to be saved in formats that are readable by spreadsheet applications such as Excel and Lotus.
	Generate Reports	Reports are provided as (ASCII) text files that can be exported into either word processors or spreadsheets.
Parameters	Mortality	Allows the editing of mortality, catchability, and monthly selectivities.
	Migration	Displays parameter data related to movement of the whiting population between movecells for each simulated year.
	Recruitment	Allows the editing of whiting recruitment values for each movecell over the simulation period
Strategy		Allows the creation of population and regulation strategies.
Simulate		Simulate provides the model execution. Multiple simulation runs are also possible. WhitSim will prompt users to save the project once the simulation is complete.
Results	Strategy Time Plots	Displays the most common model variables (Egg Production, Exploitation Rate, Biomass and Total Catch).
	GIS Output Display	Allows the detailed investigation of the simulated model parameters.
Analysis	Data Selection	This allows the selection of particular variables from the output database for use in the other analysis options. These variables can be chosen by cell or zone, and are given as yearly or monthly outputs depending on the variable.
	Curve Fitting	The Curve Fitting analysis option allows the piecewise fitting of selected model variables to a number of standard continuous curves.
	Indicator	The Indicator analysis option makes it possible to create compound variables combining any of the selected variables arithmetically using a graphical pocket calculator. These

		compound variables can be subsequently graphed or analysed.
	Statistics	Statistics allows you to carry out a range of standard statistical computations on the selected model variables.
	Basic Statistics	Provide a list of standard statistics, such as means, standard deviations, etc. for variables desired.
	Means	Provides statistical tests to compare two or more means of variables. This analysis function also includes analysis of variance and t-tests for independent and paired samples.
	Regression Analysis	This option performs linear, exponential, power and logarithmic regression on two or more variables.
	Time Series and Forecasting	Two time series function are provided; cross-correlation and auto-correlation. Cross-correlation quantify a series of correlation functions between two variables, usually time series and the auto-correlation is similar but for a single variable with itself.
Window	Cascade	The Cascade command stacks all open edit windows so each is the same size as all others and only part of each underlying window is visible.
	Tile	The Tile command arranges the open windows so they cover the entire model display area without overlapping one another.
	Arrange Icons	The Arrange Icons command leaves icons evenly spaced, beginning at the lower left corner of the model display area. All open windows must be minimised or this command is disabled.
	Minimize All	To reduce all open windows to icons.
	Close All Windows	The Close All Windows command closes all open windows in the model display area. If text was modified since the last time you saved it, a dialog box will open asking if you want to save the file before closing the window.
Help	Topics	Displays a list of topics contained within the user help system.
	Contents	Displays the user help contents file.
	Getting Started	Provides summary information to the user related to using the package.
	About	Briefly describes the WhitSim package.

13.4 Data Input Manipulation Modules

Space-specific parameters can be edited for each cell to control three aspects of the fishery model: mortality, migration and recruitment.

Mortality

A two-level hierarchy breaks down the mortality catchability variable. The first is by sector: commercial and recreational. Commercial is then broken down into a matrix of four gear types: handline, haulnet, gillnet and other. This hierarchy is appropriate for the time period up to June 1983. Beyond June 1983, the gear types are further sub-divided into three target types: effort targeted at King George Whiting (KGW); effort directed at other species; and effort not specifically directed at any particular species.

Regional Selection		Catchability		Gear Type	
<input checked="" type="checkbox"/> West Coast <input checked="" type="checkbox"/> Spencer Gulf <input type="checkbox"/> St. Vincent Gulf <input type="checkbox"/> All Spatial Cells		Spatial Cell: [] <input type="radio"/> July 76 to June 83 <input checked="" type="radio"/> July 83 Onwards		[Set Defaults] [Restore Values]	
[V] [A] [P] 1 2 3 4		Target Type <input checked="" type="radio"/> Specifically Fishing Whiting <input type="radio"/> Specifically Fishing Other Species <input type="radio"/> Not Specifically Fishing any Particular Species		4.33491171662187E-5 Handline 1.05132911389948E-5 Haulnet 2.884049936046E-5 Gillnet 6.77290273390126E-5 Other 0 Recreational	

Fig. 13.3 Input screen for Regional Selection and Catchability

For each of the two type of hierarchies (< July 83 and > June 83) the mortality dialog box (Fig. 13.3) provides the ability to view and edit the standard deviation for each of the 13 Movecells. This menu item also includes the initial male selectivity as well as the monthly selectivities (relative to January) for February to December.

Migration

Movement Matrix

Select Time Frame

1976 1998

Year: 1976

1 x summer
 2 x summer
 3 x summer
 Fish 0 - 1 yrs old
 Fish 1 - 2 yrs old

Natural Mortality

yearly instantaneous

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	0.961	0.023	0.018	0	0	0	0	0	0	0	0	0	0
2	0	0.977	0.036	0	0	0	0	0	0	0	0	0	0
3	0	0	0.946	0	0	0.032	0	0	0	0	0	0	0
4	0	0	0	1	0	0.159	0	0	0	0	0	0	0
5	0	0	0	0	1	0.391	0	0	0	0	0	0	0
6	0	0	0	0	0	0.417	0	0	0	0	0	0	0
7	0	0	0	0	0	0	1	0	0	0.035	0.04	0	0
8	0	0	0	0	0	0	0	1	0	0.108	0.068	0	0
9	0	0	0	0	0	0	0	0	1	0.076	0.267	0	0
10	0	0	0	0	0	0	0	0	0	0.617	0.067	0	0
11	0	0	0	0	0	0	0	0	0	0.163	0.559	0	0
12	0.039	0	0	0	0	0	0	0	0	0	0	1	0
13	0	0	0	0	0	0	0	0	0	0	0	0	1

Fig 13.4 Input dialog box for the Migration Matrix

The migration parameter dialog box controls the movement of whiting throughout the fishery. Fig 13.4 illustrates the migration parameter input screen. The format of the migration matrix is from *row* to *column*. For example consider movecell 1 (row one): 96.1% of whiting remain in the cell and 2.3% migrate to movecell 2 and 1.8% migrate to movecell 3, in the next time period.

Migration values are set using the movement matrix controls located above the matrix. Migration matrices are selected from the centre section (for example Fish 0-1 yrs old or Fish 1-2 yrs old) and the time frame is set using the time frame scrollbar (see Fig 13.4).

Recruitment

Movecell and year give the whiting recruitment parameter. Fig. 13.5 illustrates the input parameter mechanism. Recruitment values can be established for individual Movecells, regions (West Coast, Spencer Gulf, St. Vincent Gulf) or the entire fishery. Recruitment is set using the year edit scrollbar and the set value button. Once a value is set, that value is set for all remaining years (Fig. 13.5).

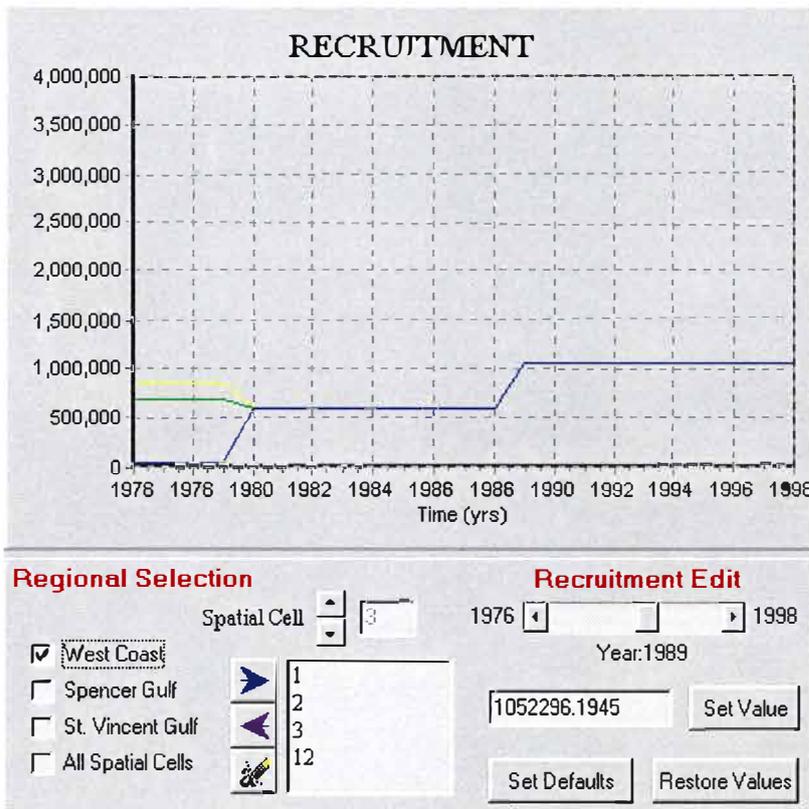


Fig 13.5 Input dialog box for selection of recruitment parameters

13.5 Strategy and Regulations

The strategy regulation dialog box provides the means by which users create and/or edit existing management strategies. Strategy variables that can be edited include the whiting legal minimum length, area and seasonal whiting quota and movecell closures, historical effort and the percentage of fishing by gear type.

Legal Minimum Length

The whiting Legal Minimum Length (LML) strategy permits the user to set the LML at any of five settings throughout the time period (270mm, 280mm, 290mm, 300mm and 310mm). The exponent (shown as *beta* in Fig. 13.6) to which the whiting population is raised in the catch equation is also provided.

The screenshot shows a control panel titled "Legal Minimum Length". On the left, there is a "Select Year Index" range from 1976 to 1998, with a "Year: 1983" label below it. In the center, five radio buttons are listed: 270 mm, 280 mm (selected), 290 mm, 300 mm, and 310 mm. To the right of these are three buttons: "Set Values", "Set Defaults", and "Restore Values". On the far right, there is a label "Exponent to which NKGW is raised in the catch equation" and a text input field containing the value "1", with the label "beta =" to its left.

Fig. 13.6 Legal Minimum Length Strategy

Area and Seasonal Whiting Quota

Fig. 13.7 displays the region and movecell selection area for editing the quota strategies. Quota changes can be made for each movecell or region within the fishing zone. A matrix (not shown in Fig. 13.7) is used to make the changes. Quota values are calculated as a percentage rating between and including 0 and 10, where 0 indicates the movecell is closed to fishing and 10 indicates that the fishing effort allowed within the area is 10 times the historical amount. Of course, a value of 1 indicates the fishing effort is equal to that of the historical values.

The screenshot shows a control panel titled "Area and Seasonal Whiting Quota". At the top right, it says "If quota is set to zero, the spatial cell will be considered closed". On the left, under "Regional Selection", there are four checked checkboxes: "West Coast", "Spencer Gulf", "St. Vincent Gulf", and "All Spatial Cells". In the center, there is a "Select Year Index" range from 1976 to 1998, with a "Year: 1976" label below it. To the right of the year selection are three buttons: "Set Values", "Set Defaults", and "Restore Values".

Fig 13.7 Area and Seasonal Whiting Quota

Regulations

Regulations Select Effort Value: 1976 1998 Set Values Set Defaults
Year: 1983 Restore Values

Proportions of Historical Effort

0.9	July	1.0	August	0.9	September	1.0	October
0.8	November	0.5	December	0.4	January	0.9	February
0.5	March	1.0	April	0.2	May	1.0	June

Percentage by Gear Type

0.2	Handline	0.4	Haulnet	0.1	Gillnet
0.2	Other	0.1	Recreational		

Fig 13.8 Regulations Sub-menu

The regulation sub-dialog box (Fig. 13.8) provides regulation strategies related to historical fishing effort and the amount of fishing effort by gear type to be set. The proportion of fishing effort can be set for each month throughout the time period, the percentage of fishing by gear can only be set yearly. Also, it is important to note that both variables are set across the entire fishing zone, there is no mechanism for setting values for individual movecells.

13.6 Analysis and Statistical Toolboxes

The analysis menu provides a number of options used to statistically analyse, summarise, and graph the output data produced by the Whiting Model. Particular variables can be selected from the output database for use in the other menu options. These variables can be chosen by cell or zone, and are given as yearly or monthly outputs. Statistics allows you to carry out a range of standard statistical computations on the selected model variables. The Curve Fitting menu option allows you to piecewise fit selected model variables to a number of standard continuous curves. Indicator makes it possible to create compound variables combining any of the selected variables arithmetically using a graphical pocket calculator. These compound variables can be subsequently graphed or analysed. Thus, Analysis allows you to choose any arithmetic combination of model output, for any set of spatial cells, and to statistically analyse and graph them.

Model Standard Outputs

The principal model outputs for assessing fishery management strategies are the time plots (time series graphs). The following describes each of these graphs and how each result is calculated.

Statistical Analysis

The Statistics menu provides a range of functions including basic statistics (frequency, descriptive and correlation statistics), mean (means, analysis of variance), regression analysis (linear, exponential, power and logarithmic) time series analysis and forecasting.

Basic Statistics

These provide a list of standard descriptive statistics including:

Table 13.3 Basic Statistical Measures

Mean	Number of observations in the data set (this is always included with the output). Mean of the data set.
Median/quartiles	First quartile (value that has 25% of the observations below it, when sorted in ascending order). Median (middle value in the data set). Third quartile (value that has 75% of the observations below it, when sorted in ascending order).
Variance	Standard deviation and variance
SE Mean	Standard error of the mean
Range	Range of values in the data set
Min and Max	Minimum and maximum values in the set
Mode	The most commonly occurring value
Sum	The sum of all the values in the data set

The following provide a measure of the shape of the distribution of values:

Table 13.4 Distribution Measures

Skewness	Measures how much the distribution is "tilted" to the left or right of the mean
Kurtosis	Measures how peaked or flat the distribution is relative to a normal curve
SE skewness	Standard error of the skewness
SE kurtosis	Standard error of the kurtosis

Correlation quantifies the similarity between two variables. For instance we would anticipate a high correlation between yearly fishable biomass and population legal start season since both would tend to rise and fall together. This option allows calculation of the standard correlation coefficient, r , between any two selected variables. The correlation coefficients can be displayed in tabular form or as a matrix.

Means and ANOVA

ANOVA statistical tests are used to compare two or more means of variables. One dependent variable and up to five independent variables can be selected. This procedure will provide a comparison of means for each combination of the one dependent variable with the chosen independent variables. Each combination is then split into groups. The following summary descriptive statistics are provided along with the ANOVA tables.

- The value of the group
- The sum of the observations that fall within the group
- The mean of these observations
- The standard deviation of these observations
- The variance of these observations
- The sum of square
- The number of these observations

If there is more than one group the following ANOVA output is listed for the Between Groups source, Linearity source, Deviation from Linearity Source and the Within Groups source:

- Degrees of freedom
- Sum of square
- Mean square
- F-statistic

If there are more than three groups the Eta-test and/or test for linearity can be performed by clicking in the appropriate boxes and produces the following:

- Eta
- Eta-square

- r
- r -square

Regression

This analysis tool allows you to test whether functional relationships exist between two variables and how accurately you can predict the value of one variable from the value of another. Plotting the variables, with the independent variable(s) along the x-axis and the dependent variable (the one being predicted) does this along the y-axis. This analysis fits a curve to the data and provides the coefficients of the fitted curve. The curves can be linear, exponential, power or logarithmic.

Time-series and Forecasting

Cross-correlation quantify a series of correlation functions between two variables, usually time series, like yearly fishable biomass, or yearly stock and recruitment. The lag is the number of years of displacement between the two series. For instance, the cross-correlation of recruitment and adult population numbers might be maximum at a lag of one year, since it would take a year for a big peak in recruitment (sublegal sized whiting) to enter the fishable stock. The cross-correlation at lag 0 is the same as the standard correlation. For a given data set, and a user-selected number of lags, this graph contains the cross correlation coefficient at lag k , and the standard error of the cross correlation function.

The auto-correlation of a time series variable is similar to the cross-correlation function, but for a single variable with itself. The auto-correlation at lag 0 is always 1, meaning the correlation of a variable with itself will always be 100%. The correlation at lag 1 measures the relative closeness of values one-year apart. A slowly varying time series will have a high auto-correlation at lag 1. Auto-correlation can be used to identify cycling time series. For instance a series with a 10-year cycle trend will have an auto-correlation peak at lag 10, because values in the series that are 10 years apart will tend to be similar. For a given data set, and a user-selected number of lags, this graph displays the sample auto-correlation coefficient at lag k , and the standard error of the sample auto-correlation is also displayed. The user has the choice of method for the standard error estimation; either Bartlett's Approximation or Independence Model, assuming errors are white noise.

Indicator Analysis

This menu option is used to create new variables that are arithmetic combinations of previously selected variables. The new compound variables can be saved and then graphed and analysed, just as standard variables are, using the Analysis menu.

Curve Fitting Analysis

Curve fitting analysis allows the fitting of any selected variable to a choice of three continuous curve functions, linear, power, or exponential. For any particular choice of function, the full range of the data series can be partitioned into as many as four subdivisions and each subdivision fitted separately. The formulae for the fitted curves can be displayed using Show Statistics or exported and printed using Create Report.

To select a variable, click the down arrow on the drop down list provided under the graph. The list of previously selected variables is displayed. Once a new variable is selected the graph will automatically change to plot this new variable.

The three sliders at the bottom of the screen can be used to divide the interval (1976-1998) into a maximum of four separate subintervals indicated by blue vertical lines on the screen. This allows the selected function to be fitted separately to each portion of graph contained in each subinterval, resulting in a closer overall fit. Because the first and second dividing lines are both initially set on the left edge of the graph (1976), it is not possible to move the first slider until the second slider has been moved. To change between the selected functions simply select the function required (lower right hand corner of the dialog box). For each function the following statistics are available:

Table 13.5 Curving Fitting Statistical Measures

r squared	a measure of the strength of the correlation of the fitted function to data
Standard Error	square root of the average squared difference between the observed and predicted y-values
SST Value	sum of the squared deviations of the observed data values from their mean
SSR Value	Amount of variation in the observed y-values that is not explained by the equation or the total squared error made in using the equation to predict the observed y-values
Standard Deviation	a measure of the spread of the distribution of data values from their mean
Number of observations	Number of observations in the data set
Linear correlation coefficient	used to describe the strength of the linear relationship between two variables
Standard Error of the Mean	displays the standard error of the mean of the observations (dependent y-variable)
Variance	the average of the squares of the deviations of the y-values from their mean
Mean	mean of the y-values

13.7 Graphical Information System

Complementing the four critical variables displayed with the time plots menu option, the graphical information system (GIS) allows the construction of time plots for the complete list of model output variables. The display of variable data in the GIS can be shown in a number of modes, which is largely controlled by the display options sub-dialog shown in Fig. 13.9. For example, variables can be displayed in *time series* or *spatial cell series* modes. Within each display mode, historical, simulated and overlay data can be displayed separately or in combinations.

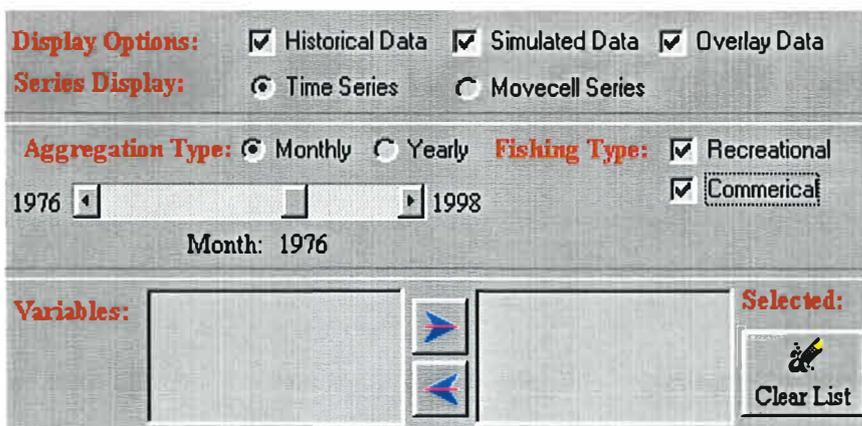


Fig. 13.9 Input dialog box for GIS data display formats

Fig. 13.10 shows the graph options sub-dialog. This sub-dialog allows you to edit the display modes of the GIS graphing section. For example, users are able to select from a number of graph types: including line graphs, bar graphs, area plots and pie graphs.

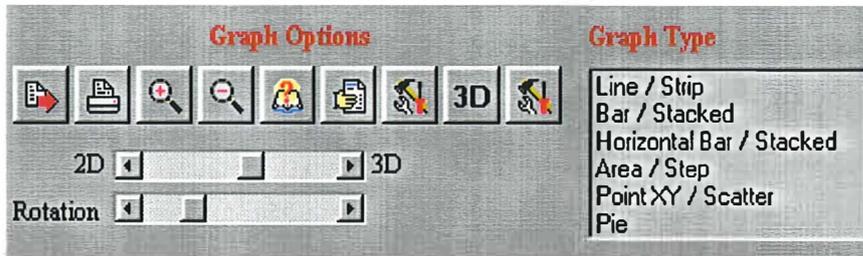


Fig. 13.10 Input dialog box for selection of Graphing display options

For additional information on the GIS module, please refer to the user help system contained within the WhitSim package.

13.8 Discussion

It is important to understand that the South Australian Whiting Fishery Management Model represents only some of what is known about the whiting fishery around the South Australian coastline. It is also important to emphasize that the model is only a tool to help fishers, scientists and managers make strategic management decisions.

Finally, the WhitSim does not accurately duplicate the real world. Rather, it is based on a number of assumptions that determine the level of confidence and certainty that can be placed in the model. The user should be aware of such limitations and realise that the model is limited to the level of understanding of the biology of the King George whiting, and the integrity of the data on which the model is based.

CHAPTER 14. BENEFITS AND STAFF

14.1 Benefits

There were two major outcomes of this project.

1. It has made a significant contribution to understanding the population biology of King George whiting. This includes knowledge of the life-history, reproductive biology, dispersion of fish with respect to size and age, stock structure, adult movement patterns, population ecology and spatial scale over which larval advection and adult movement occur.

Much of this new information has already been conveyed to managers of South Australia's fisheries through annual stock assessment reports, and is therefore available for consideration when forming management strategies. Furthermore, much of this information has also been conveyed to the Australian marine science community as scientific publications, and presentations at annual conferences. It is, therefore, available to scientists and managers working in other states on this and other related species of whiting.

2. The second outcome was the development of the age-structured, spatial, temporal fishery model for the King George whiting in South Australia. Firstly, this model provides a state-of-art, sophisticated stock assessment tool for describing population and fishery dynamics for this species. Secondly, the simulation model provides a means for testing alternative management scenarios that will strongly facilitate future stock assessments.

The South Australian Marine Scalefish Fishery is the major beneficiary of this development since the model provides a means for doing sophisticated and comprehensive stock assessments. A further benefit is that the model has provided opportunity for the development of a new generation of fishery models. The sophisticated interface developed for the King George whiting model can now be adapted for use for other species, a process which is now underway for snapper (*Pagrus auratus*) and garfish (*Hyporhamphus melanochir*) (FRDC 99/145).

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