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The fisheries biology and population dynamics of snapper *Pagrus auratus* in northern Spencer Gulf, South Australia

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Declaration

This thesis contains no material which has been accepted for the award of any degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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I would like to express my deepest thanks to Jennifer, Sam and Anna for having the patience to put up with me locked up in a study when there were better things to be doing on a weekend.

Abstract

The sparid *Pagrus auratus* has been the subject of significant commercial and recreational fishing in South Australia from the early 1950s. In the 1980s and 1990s, declining catches caused concerns about the sustainability of fishing practices, with commercial catches falling to their lowest level in 30 years in 1994/5. Most of the biological research for snapper had taken place in the late 1970s and early 1980s when fishery research on coastal finfish was first established in South Australia. Apart from a tagging programme initiated in 1987, little new work had been undertaken. The serious decline in catches prompted the need for a renewed research effort on *P. auratus* and led to the establishment of this study.

The study was conducted in Northern Spencer Gulf (NSG) where the fishery is concentrated and accounts for 50-75% of the total State commercial catch. The two broad objectives were:

1) To gain a better understanding of the fisheries biology of the species and determine whether there was a biological cause for both the decline in the commercial catches and the cycles evident in them and,
2) To integrate known biological and fishery information into a simple population model which provides a coherent depiction of the dynamics of the snapper population and which can be used to provide guidance to fishery management decisions.

The biological component of the study focused on age, growth, migration and biomass estimation. To develop age compositions of the commercial catch, an ageing process based on the sagittal otoliths was developed and tested on samples collected in 1991 and 1994/95. Multiple independent readings of annuli showed a high level of precision and no systematic bias. The deposition of annuli was observed in samples collected from November to February inclusive. A comparison of ages estimated from otolith and scale readings demonstrated a significant under-estimation of age based on the reading of scales. The maximum age of 34 years recorded increased the previous longevity estimates of snapper in South Australia by 50%. The age composition of the commercial catches showed gear dependent differences, with the handline sector catching fish from 3 – 15 years of age and the longline sector generally catching fish >

12 years. Highly variable yearclass strength was observed, with strong yearclasses in 1979 and 1991 but poor recruitment through the 1980s. It was evident that occasional yearclasses supported the fishery and that the variable recruitment was largely responsible for the fluctuations evident in the commercial catches.

As a precursor to the use of the Daily Egg Production Method (DEPM) to estimate spawning biomass, an experimental study was used to determine the development rates of snapper eggs in the temperature (18 – 24^{0}C) and salinity (36 - 48‰) ranges characteristic of NSG during spawning. The elapsed time from placing the eggs in their experimental treatments until 50% hatch varied from a minimum of 17.25 hours at 24^{0}C to a maximum of 33.75 hours at 18^{0}C. Although the effect of salinity on incubation period was not statistically significant, there was a consistent small increase in incubation period of 1 – 1.5 h within each temperature with an increase in salinity from 36 - 48‰. There was no significant difference in the effects of temperature or salinity on the proportion of eggs which hatched or the viability of larvae which hatched.

The data collected from the concurrent sampling of plankton and adult snapper was used to estimate spawning biomass using the DEPM. Snapper eggs were enumerated from plankton samples collected throughout NSG in November and December 1994, December 1995 and January 1996. Egg distribution was not consistent between sampling periods and spawning areas were only loosely defined. It appears that spawning is most common in the central to western part of NSG, in the area south of Whyalla and north of Cowell. The ovaries from adult female snapper from this area also showed a greater proportion of advanced oocyte development. Egg production was estimated to range from 1.19 eggs.m^{-2}.day^{-1} in November 1994 to 4.17 – 4.68 eggs.m^{-2}.day^{-1} in the two December surveys. No estimate was possible in January 1996 as the sample of eggs did not cover the distribution of ages necessary to estimate egg mortality and egg production. The ageing of individual eggs showed a peak spawning time between 1700 and 1800 hours although some sporadic spawning apparently occurs throughout the day.

Gonad samples supported a size at first maturity of 23 cm LCF and a sex ratio of close to 50%. The proportion of mature females with hydrated oocytes or post-ovulatory follicles varied markedly throughout the study area, with samples ranging from 0 – 100%. The proportions were generally low in the northern and eastern samples, and were consistently higher in the south-western samples. Batch fecundity was estimated as $F = 21,992 + 36,189^{*}$ weight (kg) ($r^2 = 0.50$). A new length weight relationship of whole weight (kg) = $5.958 \times 10^{-5} * \mathrm{LCF}\ (\mathrm{cm})^{2.692}$ was determined from 529 fish samples, with no significant difference between males and females. The difficulties of obtaining adequate spatial coverage for the adult samples limited the estimation of spawning biomass to the December 1994 survey, and was further restricted to a sub-region of the study area. The estimate of biomass was 1,318 tonnes with bootstrapped 95% confidence intervals of 448 – 1,549 tonnes.

The concept of “resident” and “migratory” components to the population has previously been proposed for snapper in Australia and New Zealand. Tagging studies have consistently shown that the majority of snapper were recaptured in close proximity to their release site, but that some long distance movements occurred. The possibility of a resident population in Spencer Gulf supplemented by an annual influx of migratory fish from shelf waters has important implications for fisheries management. A re-analysis of tagging data used a movement model to estimate residency and annual movement rates between NSG, Southern Spencer Gulf (SSG) and shelf waters, including size related differences in those parameters, and investigated the seasonality of those movements into and out of NSG. Residency rates of 57 – 60% and were estimated for NSG and SSG respectively. Total emigration from NSG was estimated at 31% and return immigration to NSG was estimated at 6.3% for fish < 5 years. There was a relatively high 30 – 40% residual in these analyses, suggesting that a large proportion of snapper are migrating to low fishing effort areas where they are not subject to recapture.

The growth rates of snapper were estimated from length at age data based on ages derived from otoliths and from tag recapture information, and the estimates from the two sources of data were compared. Growth from the age length data was best described by the generalized von Bertalanffy growth function $Length\ (t_i) = 90.19 * \left(1 - e^{-0.194(t-(-2.86))}\right)^{3.211}$. The asymptotic length of 90.19 cm LCF conformed well with recorded length data and the estimate of *K* of 0.194 was the highest of published estimates for *P. auratus*. A seasonality function improved the likelihood of the fit of the growth model and estimated that maximum growth occurred in late February when water temperatures are near their peak. The analysis of growth based on tag recapture data suggested that growth was adversely affected by tagging, with estimates of growth rates that were 11 – 15% lower than estimates from age length keys. Growth was particularly affected in fish tagged with loop tags, where growth models no longer conformed to the von Bertalanffy growth function. Analyses from both sources of data showed strong evidence of highly variable growth between individuals, a factor which has masked strong yearclasses in previous length based studies.

The biological data relating to age composition, growth and migration rates were integrated with fishery catch and effort data into an age structured, dynamic model of the NSG snapper population. The model was fitted to combinations of catch at age, CPUE of the handline fishery and the December 1994 spawning biomass estimate using maximum likelihood, and model outputs estimated annual recruitment from 1979 to 1997 and spawning biomass from 1983 to 2000. Spawning biomass estimates showed a decline from 1983 to a low of approximately 1,000 t in 1992 and followed by a strong increase to 3,000 t in 2000. This pattern generally follows the commercial handline catches over that time period. The model was also tested with the addition of an age specific return migration from shelf waters, and the fit of the model improved when it included immigration of fish ages 9 – 12 years. Model yield exceeded surplus production throughout much of the 1980s leading to stock decline, but rebuilding has occurred since 1995. Annual recruitment estimates showed strong yearclasses in 1979, 1991 and 1997 and a series of weak yearclasses through the 1980s.

The population was also projected from 2000 to 2020 assuming a similar distribution of recruitment strengths to the period 1979 to 1997 and fishing mortality of $F_{0.1}$ and $F_{0.125}$. The projected biomass was then assessed against a number of biological reference points (BRPs) using probabilities determined from 100 iterations of the model projection. The estimates for overall spawning biomass B_{sp} were determined largely by the biomass of fish aged 3 – 15 years. There was a >85% probability of B_{sp} exceeding 1,213 tonnes and > 60% probability of exceeding 2,052 tonnes in 2020 with either $F_{0.1}$ or $F_{0.125}$. Those tonnages represented the minimum and mid-point biomasses estimated during the period 1983 to 2000 respectively. It was therefore concluded that the outlook for the fishery was promising, with particular confidence in the period to 2010 when known strong yearclasses would still be present in the catch. Confidence in the period beyond 2010 will depend on continued occasional strong yearclasses to support the fishery.

Chapter 1. Introduction

1.1 Background

1.1.1 The species

The Sparidae is a diverse family of fishes encompassing 29 genera and more than 100 species (Nelson 1984). The species are predominantly marine although a small number inhabit brackish waters and 2 are known to enter fresh water. They are distributed throughout tropical, sub-tropical and temperate waters of the world's oceans. Four sparids have distributions which include southern Australian waters: the yellowfin bream *Acanthopagrus australis*, the black bream *A. butcheri*, the tarwhine *Rhabdosargus sarba* and the snapper *Pagrus auratus*. This diversity is very limited compared to the 22 genera and 41 species that occur throughout the temperate waters of southern Africa (Smith et al. 1986) but all form the basis of commercial and recreational fisheries and are therefore economically important (Kailola et al. 1993).

The subject of this study is *Pagrus auratus*, known in South Australia as snapper. The species is widespread in the western Pacific and has non-overlapping southern and northern hemisphere distributions (see 2.3.1 for discussion of taxonomy). The southern hemisphere populations of *P. auratus* are distributed across southern Australia and the north island of New Zealand (MacDonald 1982). More specifically, the Australian distribution extends from the tropical waters of Western Australia near Barrow Island, continuously around the southern coastline and north to Queensland waters near Rockhampton. In New Zealand, *P. auratus* is found in all coastal waters of the North Island and in northern parts of the South Island, where they are one of the most abundant demersal species (Kendrick and Francis 2002; Francis et al. 2002). The populations of the southern hemisphere therefore occur throughout a latitude range of approximately 25^0, from 15^0S to 40^0S.

In the northern hemisphere, snapper are found in the South China Sea from the southern islands of Japan, the coastlines of China, Taiwan, Hong Kong, Vietnam and the northern islands of the Phillipines (MacDonald 1982).

1.1.2 Concerns in the fishery

P. auratus is the subject of commercial and recreational fishing throughout its Australian range (Kailola et al. 1993). In South Australia, commercial catches are recorded back to the first records of the early 1950s (Jones et al. 1990). Concerns about the sustainability of fishing practices on the species were raised in the 1980s and early 1990s when commercial catches declined significantly. This decline was first observed in southern Gulf St Vincent, where commercial catches halved from > 80 tonnes to < 40 tonnes in the five years to the end of the 1980s (Fig. 1.1). They continued to decline until a low of approximately 10 tonnes in 1994/95. The decline in southern Gulf St Vincent contributed to a serious decline in the total State catch in the early 1990s, falling to its lowest level in 30 years in 1994/5 (Fig. 1.2).

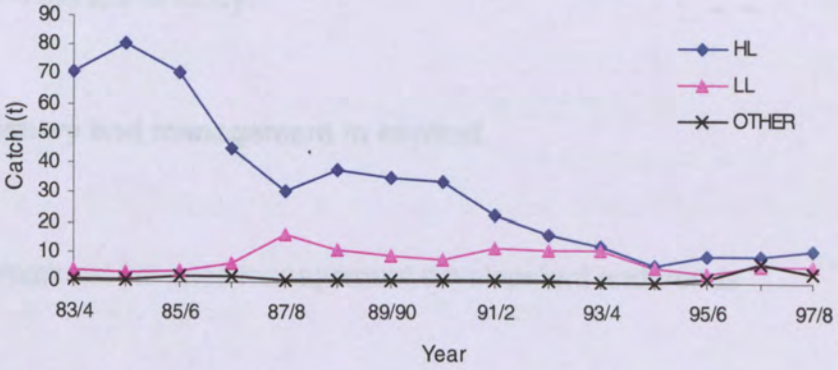


Fig. 1.1 Trends in annual snapper catches by method in southern Gulf St Vincent from 1983/4 - 1996/7. HL handline, LL longline (from McGlennon and Jones 1997).

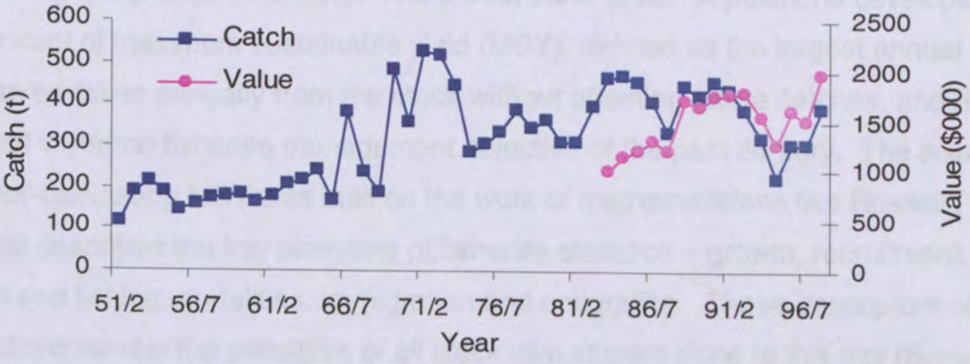


Fig. 1.2 Total South Australian snapper catch (1951/2 - 98/9) and value (1983/4 – 98/9) (from McGlennon and Jones 1999).

The biology of *P. auratus* had been studied since the late 1970s in South Australia (summarised in Jones 1981; Jones 1984a; Jones 1987; Jones et al. 1990; Rohan et al. 1991). The fisheries management of the species was based on this body of local knowledge together with information from other Australian and international studies. Stock assessments had utilised yield and egg per recruit models to assess optimum levels of fishing mortality (exploitation rates) and to set minimum size limits (Jones 1984a; Jones 1987; Jones et al. 1990; Rohan et al. 1991). However, the stock assessment and research information available to fisheries managers could not adequately explain the decline in catches observed during the early 1990s.

Most of the biological research for snapper had taken place in the late 1970s and early 1980s when fishery research on coastal finfish was first established in South Australia. Apart from a tagging programme initiated in 1987, little new work had been undertaken. The serious decline in catches prompted the need for a renewed research effort on *P. auratus* and led to this study.

1.2 The fishery and management in context

1.2.1 International fisheries management development and trends

Fisheries management has existed as a discipline for at least 120 years, from the period in Europe in the mid to late 1800s when variations in catches were first observed (Smith 1988; Neilsen 1999). Through the first half of the 1900s, the idea that natural resources were like crops to be planted, managed and harvested dominated the thinking of fisheries scientists. The efficient use of fish populations developed into the concept of maximum sustainable yield (MSY), defined as the largest annual catch that can be taken annually from the stock without affecting future catches, and became the most common fisheries management objective of the past century. The scientific basis for calculating MSY was built on the work of mathematicians like Russell (1931) who first described the key elements of fisheries statistics – growth, recruitment, natural and fishing mortalities, immigration and emigration. These descriptors of fish populations remain the principles of all stock assessment done to this day (Sissenwine et al. 1988).

The theory of underpinning biological targets such as MSY were derived from deterministic single species models. However, the large variability in catches and stock recruitment relationships evident when attempting to manage fisheries on this basis have shown the limitations of this theory (Collie and Spencer 1988; Caddy and Mahon 1995). Over the past 50 years, fisheries management on maximum sustainable yields of single species has evolved to a multidisciplinary ecosystem management approach (Caddy and Mahon 1995; Neilsen 1999; Kruger and Decker 1999). In addition to the limitations of MSY, this has occurred through the addition of three other disciplines to the narrow biological focus inherent in MSY management – economics, sociology and ecology.

The biological focus was first challenged in the 1950s by economists who argued that economic value must also be maximised. They had observed that a fishery in which the economic return from catches was matched by the outlay in costs, yielded no value. This concept led in turn to the development of limited entry fisheries, where access to stocks are restricted in order to keep fishing effort and costs down, and therefore increase profits. In the 1960s, as recreational fisheries expanded, it was argued that simple biological and economic objectives were no longer adequate. Recreational fishers derived "value" from a fishery in which they received aesthetic pleasure, such as enjoyment of the outdoors, companionship of others, physical activity and travel, as much as the harvest they took home.

The latter two decades saw the development of broader biological and then ecological objectives, from the single species management to multi-species management to ecosystem management. The development of multi-species management was driven by the recognition from fisheries biologists that the ecological relationships of their "single species" could not be managed in isolation. The progression from multi-species to ecosystem management was a logical next step, and was an acknowledgement that fisheries must be thought of as communities or at least as interacting groups of populations (Grumbine 1994; Lackey 1995; Kruger and Decker 1999). The movement was also due, at least in part, to the influence of international forums such as the 1992 United Nations Conference on the Environment and Development (UNCED) (Caddy and Mahon 1995). It also reflected both a more general appreciation of the need to sustain ecological diversity and function, as well as evidence that some single species fisheries, which had received substantial investments of research and management resources, continued to perform poorly.

The addition of economic, sociological and ecological objectives into fisheries management saw the proposed demise of MSY (Larkin 1977), although others argued that it remained useful as a limit reference point (Shepherd 1999). However, the search for a simple replacement objective for MSY has been largely unsuccessful. Proposals such as optimum sustainable yield (OSY), which recognises a broad group of goals (Neilsen 1999), have had limited acceptance (King 1995). OSY allows for fishery specific objectives to be defined, recognising the diversity of fisheries, fishers and fish which exist, but demands significantly greater inputs for decision making. A more recent and promising advance has been the use of multiple reference points which can be fishery specific (Caddy and Mahon 1995). Further, the development of multi-species and ecosystem models has been slow and has not provided the predictive power needed for most fisheries management (National Research Council 2002).

1.2.2 Trends in fisheries stock assessment

Stock assessment is the scientific and statistical process whereby the status of a marine fish population is assessed in terms of population size, reproductive status, fishing mortality, and sustainability. As fisheries management objectives have broadened, and fishing pressures increased, demands for more sophisticated stock assessments have also increased. The original population dynamics functions of growth, recruitment and mortality have been developed into increasingly sophisticated stock assessment methods over the past 50 years (Beverton and Holt 1957; Ricker 1975; Gulland 1983; Hilborn and Walters 1992; Quinn II and Deriso 1999, and others).

Modern stock assessments are generally based on population models of one of three classes (Sissenwine et al. 1988): 1) spawner – recruit, 2) dynamic pool or 3) production models. All treat the 4 population dynamic functions with varying degrees of aggregation or specificity. Spawner – recruit models deal only with recruitment and describe the relationship between generations. Dynamic pool models deal with changes in biomass following the recruitment of a cohort, and allow age-specific growth and mortality to be modelled. Production models aggregate the dynamics and describe the effects in a single function. In a population where inter-annual recruitment variability is high, the changing age composition results in dynamic growth rates, mortality and fecundity and therefore limits the use of these models.

Age-structured dynamic pool models therefore offer the most adaptable alternative to tailor the characteristics of a population and fishery (Sissenwine et al. 1988). Models which add simulation techniques, such as Monte Carlo trials, provide estimates of the risks of different management strategies.

1.2.3 This study in context

Despite the trend towards multiple objective management regimes, and towards ecosystem management, research on the biology of single species continues for two important reasons. Firstly, an understanding of the biology of each species underpins the broader multi-species approach ie. multi-species management is, at its simplest, the sum of a number of single species studies plus an understanding of how the species interact (Van Den Avyle and Haywood 1999). Secondly, fisheries management agencies generally do not have the authority to manage the diverse components of the aquatic ecosystem and are strongly driven by the focus of the single-species interests of recreational and commercial fishing industries (Schramm and Hubert 1999).

This study on snapper provides such a single species stock assessment. Although snapper is captured in a multi-gear, multi-species fishery, the majority of the snapper catch is targeted by specific fishing gear and in specific locations. It can, therefore be managed as an individual species, albeit as one component of a more general fishery. The stock assessment techniques of an age structured biomass (dynamic pool) model built on biological data on growth, migration, age structure and biomass provides the most comprehensive assessment possible. And the simulation modelling techniques used allow a quantitative predictive capacity not previously available to fisheries managers.

1.3 Objectives of the study

The study had two broad objectives:

1) To gain a better understanding of the fisheries biology of the species and determine whether there was a biological cause for both the decline in the commercial catches and the cycles evident in them and,

2) To integrate biological and fishery information into a simple population model to provide a coherent depiction of the dynamics of the snapper population to be used to provide guidance for fishery management decisions.

In order to address the biological questions, the study focussed on the following areas:

a) Ageing and age structure of the population
    i) One potential explanation for the cycles (and decline) may have been variable recruitment. No direct recruitment studies had been undertaken in South Australia but age structure analyses using scales as the ageing medium had concluded that there was no evidence of variable recruitment (Jones 1981). However, variable recruitment had been reported in *P. auratus* populations in New Zealand and Victoria (e.g. Francis 1993; Davies and Walsh 1995; Coutin 1997). This study used otoliths to develop population age structures to assess (among other things) the evidence for inter-annual variability in recruitment;
b) Growth
    i) Previous analyses of growth were also based on direct ageing using the scales from individual fish. Here, the description of growth required the reanalysis of ages from otoliths, involving the development of new growth equations for population modeling;
c) Migration
    i) The life history of snapper in Spencer Gulf had long been postulated to involve a combination of resident and migratory fish (Jones 1984a; Jones et al. 1990; McGlennon and Jones 1997). The variable influx of migrants could also potentially contribute to cycles observed in the catches. Tagging studies had generally provided qualitative descriptions of movement (Jones 1984a), but had not determined the quantitative rates of residency and migration. This study used a movement model to make the first estimates of these rates;
d) Spatial spawning patterns
    i) Although snapper were known to spawn in Spencer Gulf from October to February (Jones 1981), the patterns of spawning were poorly understood. As a consequence of the plankton method of estimating biomass (see below), spatial patterns of egg production were determined as were batch fecundity estimates and a new length / weight relationship.

The second primary focus of this study was to generate a population model that integrated the new biological information with fishery information to provide a means for interpreting the changes in biomass over the period when catch declined. It was also intended to use the model to make projections into the future, and to assess future risks to the fishery and to the stock. The model was purposely built in MS Excel to use a tool which is within the reach and understanding of most fisheries biologists, as opposed to more complex software such as Mathematica and AD Model Builder which require intensive mathematical and programming input.

e) To scale the model biomass trajectory, the study used a fishery independent method to provide an estimate of biomass at one point in time. The Daily Egg Production Method (DEPM) has been extensively used in clupeoid fisheries (Alheit 1993) and was advocated as suitable for *P. auratus* (Zeldis 1993). This was the first attempt to produce an independent estimate of biomass using their method for any species in South Australia.

This study was initiated in 1993 with the main fieldwork for the study conducted from 1994 to 1997. Analyses also utilised a) data from a tagging programme for which the author assumed responsibility in 1990 and b) otoliths collected by the author in 1991 that were used to develop age structures for that time. The analysis of data collected for the study continued until 2002, with the population model developed as the final component in 2002 and 2003. The author relinquished responsibility for snapper research at SARDI in 1999. The model has therefore used information available until that time, with the exception of the published age structure for the year 2000 (used with the permission of Dr Tony Fowler, SARDI, who assumed responsibility for the programme after my departure) and published fishery information in 2000. Information on the South Australian fishery published after 2000 has not been incorporated in this study but is referred to in the discussion of individual Chapters where relevant, and in Chapter 9, General Conclusions and Discussion.

1.4 Thesis structure and content

The thesis contains eight additional chapters and is structured as follows;

Chapter 2 contains background information on the study area of northern Spencer Gulf and the commercial and recreational fisheries for snapper in South Australia. The fisheries information provides important context for the interpretations of length distributions and age composition of the commercial catch in Chapter 3, and for the population modeling in Chapter 8. Chapter 2 also contains an overview of the biology of *Pagrus auratus* with particular reference to aspects of relevance to this study.

Chapter 3 documents the length frequency distributions and age composition of gear-specific sectors of the commercial catch. An ageing methodology using sagittal otoliths was developed and evaluated, and the resulting age compositions were used to interpret trends in fishery catches and to comment on recruitment variability.

Chapter 4 describes an experimental approach to evaluate the effect of temperature and salinity on the development rate of snapper eggs. The experimental temperature and salinities reflected those found in the hypersaline environments of northern Spencer Gulf during the summer spawning season. The development rates then provided a key for assigning ages to snapper eggs collected in the field during the study described in Chapter 5. The study also investigated the effects of the experimental conditions on hatching proportions, larval viability and larval length.

Chapter 5 describes a study that provided an independent estimate of spawning biomass using the daily egg production method (DEPM). The study collected plankton samples during two spawning seasons and used the data to estimate total snapper egg production in the study area. Concurrent sampling of adult snapper provided estimates of sex ratio, batch fecundity, age at first maturity, proportion of females that were spawning and mean size of mature fish. The estimated parameters for adult fish and the estimates of egg production were then used to estimate spawning biomass.

In Chapter 6, tag recapture information is used to estimate the rates of residency, emigration and immigration in northern Spencer Gulf. The data from the tagging programme had previously been used to provide qualitative information on snapper movements but this study provides quantitative estimates for use in the population model of Chapter 8.

Chapter 7 re-evaluates the growth of snapper using the age length keys arising from the age composition study in Chapter 3, and compares the results with estimates of growth parameters generated from the tag recapture information. The study also disaggregates information from the two types of tags used and evaluates the effect of tags on growth.

Chapter 8 integrates the age composition, growth and migration estimates from Chapters 3, 6 and 7 with fishery statistics into an age structured population model. The model is fitted to catch at age data, the estimate of biomass from Chapter 5 and to fishery catch rates. It estimates yearclass strength from 1979 to 1997 and biomass from 1983 to 2000. The population is then projected forward to 2020 using the model inputs and estimates of annual recruitment, and evaluates the probabilities of meeting a number of biomass related reference points.

Chapter 9 concludes the thesis with a summary of the key results for each Chapter and comments on areas of future research. It then discusses the overall results of the study and draws general conclusions.

Chapter 2. Description of the South Australian fishery for snapper, *Pagrus auratus*, the study site of northern Spencer Gulf and an overview of snapper biology.

This chapter provides background information on the commercial and recreational fisheries for snapper, *Pagrus auratus*, in South Australia and the study site of northern Spencer Gulf. It also provides an overview of snapper biology with particular reference to aspects of relevance to this study.

2.1 Study area - northern Spencer Gulf (NSG)

P. auratus is caught by commercial and recreational fishers throughout the coastal waters of South Australia. However, catches are not distributed evenly throughout the State. Generally, 85-90% of the Statewide commercial catch has been taken in Spencer Gulf of which 70 – 90% has been taken in northern Spencer Gulf (north of latitude 34^{0}S) (McGlennon and Jones 1997). Thus, given the dominance of this region's influence on Statewide trends, this study was concentrated on northern Spencer Gulf (Fig. 2.1).

Spencer Gulf occurs approximately midway along the southern coast of Australia between longitudes 136^0 and 138^{0}E and runs approximately north – south between latitudes 32.5^0 and 35^{0}S. It is approximately 300 km long and 80 km wide at the entrance. Spencer Gulf is an inverse estuary, characterized by high summer temperatures, high evaporation and little or no freshwater inflow (Shepherd 1983; Nunes and Lennon 1986; Petrusevics 1993). The Gulf has a mixed semi-diurnal tidal pattern with a tidal period of 12.5 hours, and a tidal range of up to 3m (Shepherd 1983). The strong tides generally yield a homogenized water body from surface to seabed away from the entrance (Bullock 1975). Water temperatures range from 15^{0}C to 24^{0}C in the southern basin (south of 34^{0}S) and from 11^0 to 26^{0}C in the northern Gulf (Shepherd 1983; Nunes and Lennon 1986). Salinities range from 36‰ in the southern basin to 45 - 48‰ in the northern extremes of the Gulf in late summer (Shepherd 1983).

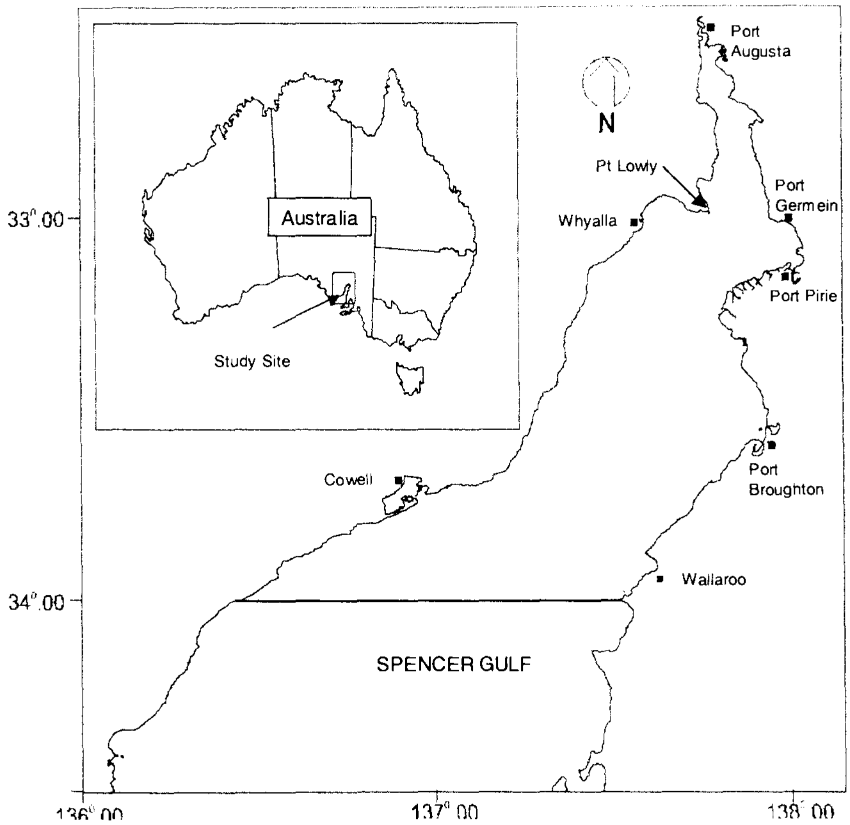
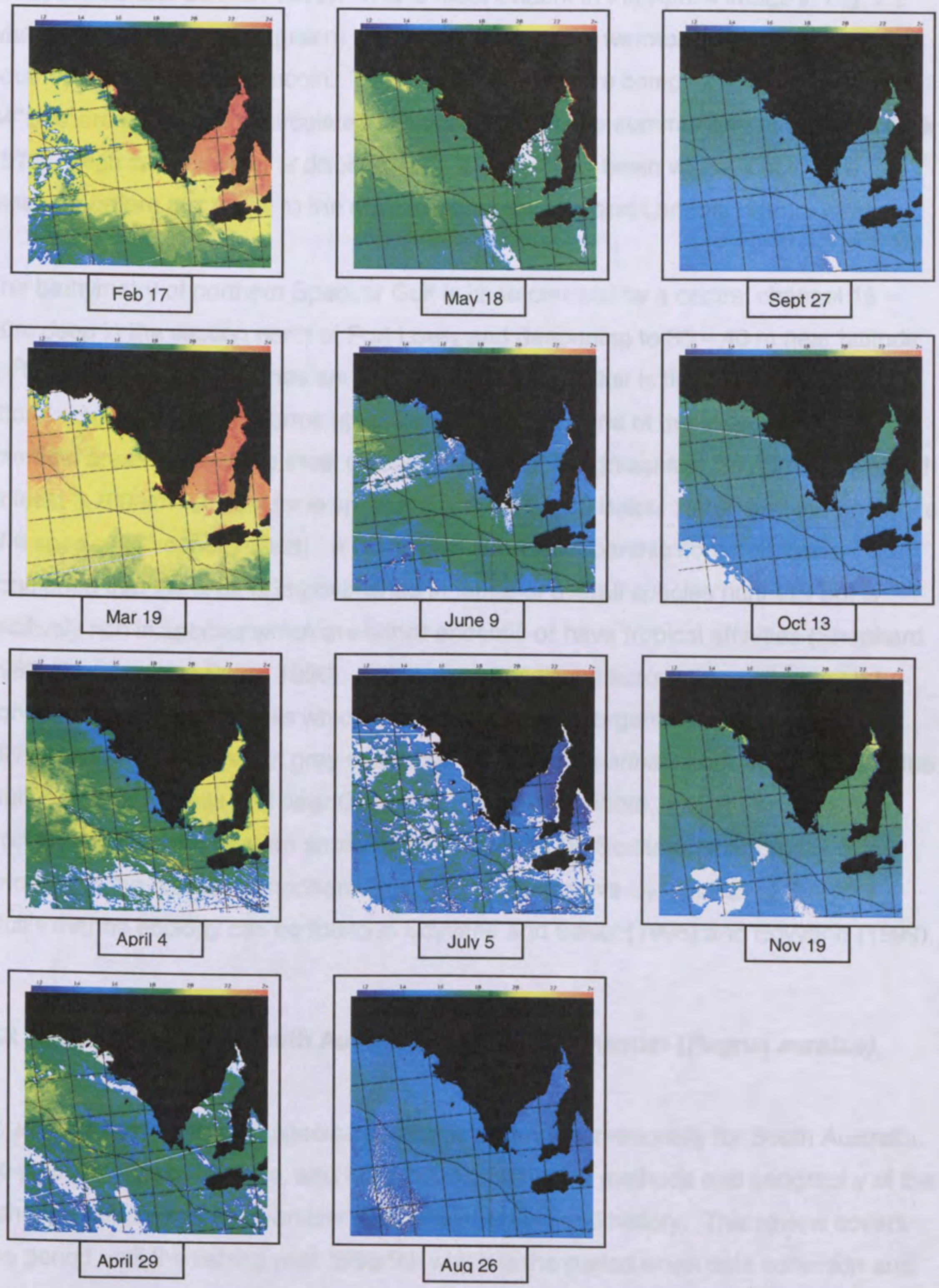


Fig. 2.1 Location of study area; Spencer Gulf, South Australia north of latitude 34^{0}S.

The seasonal changes in water temperatures are evident in the satellite images for the period February to November 1998 (Fig. 2.2). Peak temperatures of 25^{0}C are evident in February and March in the northern Gulf and are at least 5^{0}C warmer than adjacent shelf waters. The images show evidence of a temperature front at the entrance to the Gulf from February to early April in this year. Gradients of 3 – 3.5^{0}C have been recorded in surface temperatures across this front and of 7 – 8^{0}C in benthic water temperatures (Petrusevics 1993). The front reduces water exchange between the Gulf and the shelf during summer and autumn (Bullock 1975; Nunes Vaz et al. 1990; Petrusevics 1993). The temperature gradient then breaks down in autumn (note change from April 4 to 29 in Fig. 2.2) and results in a discharge of high density, saline water to the shelf, the signature of which remains evident to the shelf break at depths to 300m (Nunes and Lennon 1986; Lennon et al. 1987).



Feb 17

Mar 19

April 4

April 29

May 18

June 9

July 5

Aug 26

Sept 27

Oct 13

Nov 19

Fig. 2.2 Sea surface temperature in Spencer Gulf, Gulf St Vincent and shelf waters from February to November 1998. The colour scale on each image ranges from 12^{0}C (deep blue) to 25^{0}C (red).

Temperature salinity profiles provide evidence that shelf waters enter the Gulf along the western shore and then circulate in the southern basin in a clockwise gyre (Bullock 1975; Nunes and Lennon 1986). This is most evident in the April 4 image in Fig. 2.2 where a tongue of cooler (green) water intrudes into the warmer (yellow) water of the southern Gulf near Port Lincoln. The flow pattern is more complex north of latitude 34^{0}S where it appears to circulate in vertical gyres in late summer and autumn (Bullock 1975). High salinity water is discharged to the southern basin where it acts as a reservoir before discharge to the shelf in winter (Nunes and Lennon 1986).

The bathymetry of northern Spencer Gulf is characterized by a central channel 15 – 20m deep in the section north of Port Lowly and deepening to 30 – 40 m near latitude 34^{0}S (Shepherd 1983; Nunes and Lennon 1986). The Gulf is flanked by broad sub-littoral – supra-littoral platforms up to 2 km in width in parts of the eastern shore. The intertidal areas support the most extensive areas of seagrasses in South Australia, with at least 3,700 km^2 of *Posidonia* sp. alone (Edyvane and Baker 1996), and the presence of 6 species (Shepherd 1983). A number of surveys of benthic flora and fauna concluded that the area is impoverished in terms of overall species richness but is relatively rich in species which are either endemic or have tropical affinities (Shepherd 1983, Edyvane and Baker 1996). Tributary channels cut across the platforms and connect to mangrove creeks which are rich in decaying organic matter (Butler et al. 1977). Extensive forests of grey mangrove (*Avicennia marina*) occur at the head of the Gulf, south of Whyalla and near Cowell on the western shore, and at Port Pirie and Port Germein on the eastern shore (Butler et al. 1977). Scattered mangroves occur throughout the rest of the northern Gulf. A more extensive description of Spencer Gulf's marine ecology can be found in Edyvane and Baker (1996) and Edyvane (1999).

2.2 Description of the South Australian fishery for snapper (*Pagrus auratus)*

P. auratus is an important species economically and recreationally for South Australia. To place this in perspective, and to introduce the fishing methods and geography of the fishery, I will provide an overview of its management and history. This review covers the period until the fishing year 1998/99, which is the period when data collection and fieldwork were completed for this study, and uses data and figures prepared for Fishery Assessment Reports during that period (McGlennon and Jones 1997; McGlennon and Jones 1999; McGlennon 1999). More recent management changes and fishery trends will be incorporated in the discussion in Chapter 9.

2.2.1 Fisheries management for *P. auratus* in South Australia

The history of fisheries management of *P. auratus* in South Australia can be found in a number of discussion papers prepared by officers in the Department of Fisheries (Jones 1984a; Jones 1984b; Jones 1987; Jones et al. 1990; Rohan et al. 1991), and in Fishery Assessment Reports by the South Australian Research and Development Institute (McGlennon and Jones 1997; McGlennon and Jones 1999; McGlennon 1999; Fowler 2000).

P. auratus is predominantly captured by commercial fishers in the Marine Scalefish Fishery (MSF). The MSF is a limited-entry fishery with licence transferability and an owner operator policy. The fishery operates throughout the coastal waters of South Australia and is considered a multi-gear, multi-species fishery. Fishers are regulated by licence conditions that govern (principally) the type and quantity of fishing gear that they can use. Two principal geartypes are used to capture *P. auratus* – handlines and longlines. Handlines are the typical hook and line fishery common to fisheries throughout the world with the line set vertically from the fisher's boat and with the baited hooks near the seabed. Longlines consist of a number of baited hooks attached to a longer, heavier line that is weighted and set along the seabed. Typically, this is retrieved the following morning. Both methods use fish bycatch, squid (*Sepioteuthis australis*) and cuttlefish (*Sepia apama*) for bait, while handlines are also baited with cockles (*Donax deltoides*) and razorfish (*Pinna bicolor*). A haul net fishery for *P. auratus* existed prior to 1993, with an annual quota of 40 tonnes in northern Spencer Gulf, but this method has since been banned.

The recreational snapper fishery is regulated by size, bag and boat limits. A size limit of 38 cm total length (≈ 32-33 cm fork length) applies in all waters. Bag and boat limits apply as follows (all lengths are total lengths):

- fish > 60 cm
  - bag limit of 2 - all waters
  - boat limit of 6 – all waters
- fish 38 – 60 cm
  - bag limit of 5 and boat limit of 15 – Gulf St Vincent, Backstairs Passage and Investigator Strait
  - bag limit of 10 and boat limit of 30 – all other waters

The snapper fishery has been managed as a single stock (Jones et al. 1990), although geographic differences exist in some of the management measures (eg. recreational bag limits). Management has included input controls such as longline hook numbers and net sizes for commercial fishers, and output controls such as size and bag limits for recreational anglers and quotas for the netting sector of the commercial sector.

2.2.2 Commercial Fishery

Commercial fishers are required to submit monthly catch and effort returns as part of the legislative responsibility under their fishing licences. Information is collected on fishing effort, species targeted and caught, fishing gear (type and number) used, and geographic location of fishing, and collated into a database known as GARFIS. The data collected from these returns forms the basis of much of our understanding of the fishery. The spatial accuracy of these data was improved with the introduction of more detailed forms in 1983/84. The State's waters are subdivided into spatial blocks (Fig 2.3) that are aggregated into 5 regions for reporting purposes (Table 2.1).

Table 2.1 Regions of South Australian waters and the corresponding GARFIS blocks

Region	GARFIS blocks
Northern Spencer Gulf (NSG)	11, 19, 20, 21, 22, 23
Southern Spencer Gulf (SSG)	29, 30, 31, 32, 33
Northern Gulf St Vincent (NGSV)	34, 35, 36
Southern Gulf Vincent and Investigator Strait (SGSV & IS)	40, 41, 42, 43, 44
West Coast and other (WC)	8, 9, 10, 15, 16, 17, 27, 28, 39

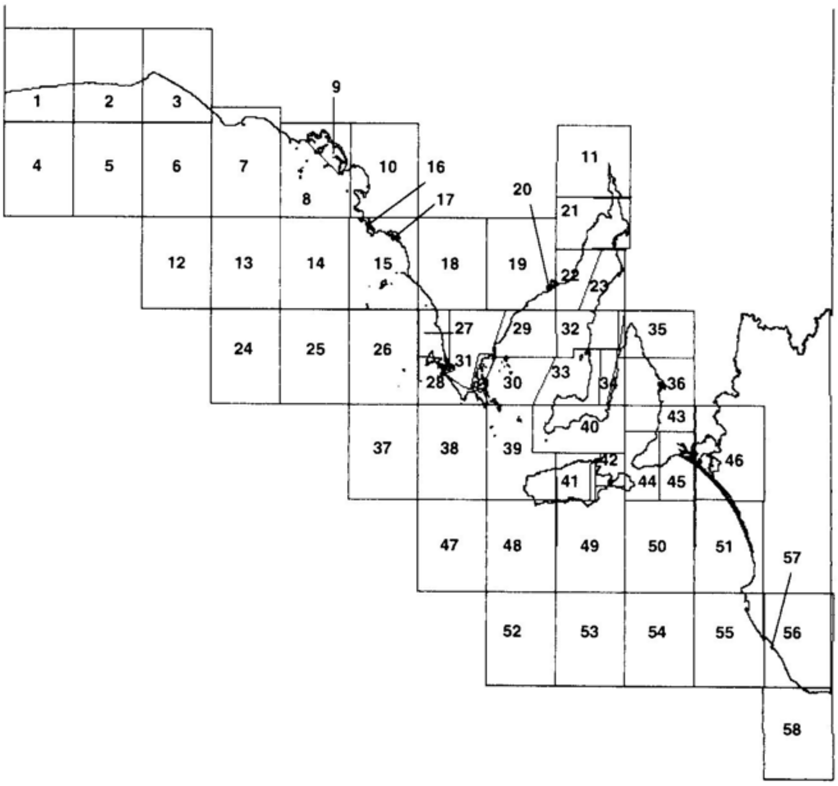


Fig. 2.3 South Australian Marine Scalefish Fishery (MSF) blocks used to report catch and effort information.

The State commercial snapper catch has ranged from 114 - 528 tonnes since 1951/2 (Fig. 2.4). The catch appears to go through cycles of increase and decline, with 2 strong cycles from 1982/3 to 1987/8 and then from 1987/8 to 1994/5. Another upward cycle is evident to 1998/99. It is noteworthy that the catch of 223.2 tonnes in 1994/5 was the lowest in 30 years. It was this decline that led to serious concerns about the sustainability of existing fishing practices. The value of the commercial snapper fishery climbed strongly from about $1m in 1983/4 to $1.8m in 1992/3 but then declined to $1.28m as catches declined (Fig. 2.4). Total value increased again to $2.24m in 1998/99.

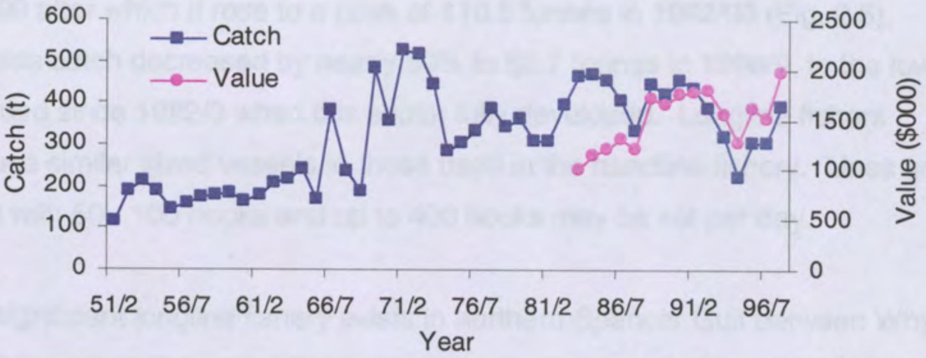


Fig. 2.4 Total South Australian snapper catch (1951/2 - 98/9) and value (1983/4 – 98/9) (from McGlennon and Jones 1997).

The handline sector of the commercial fishery contributed the greatest proportion of the total catch in all years from 1983/4 to 1998/99 (Fig. 2.5) and is responsible for the major variation in annual catch. The handline catch has varied from a low of 142.2 tonnes in 1994/95 to a high of 380.0 tonnes in 1998/99. Vessels in the handline fishery are generally 5 - 8 metres in length, although there are some larger vessels used. Handlining is done during the day and/or night in northern Spencer Gulf but is generally a day fishery in other State waters. The handline sector fishes predominantly in late spring / summer and targets spawning aggregations of fish. In general, targeted catch and effort is highest in the summer (November to January) and then steadily declines to a low in July.

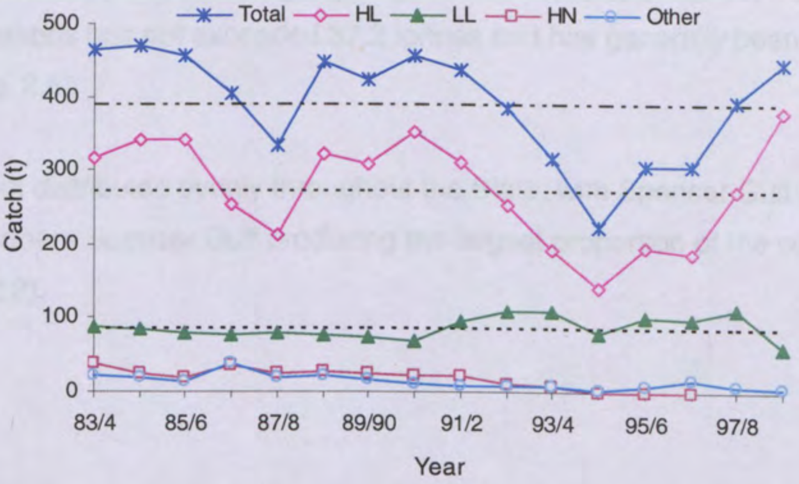


Fig. 2.5 Annual commercial snapper catch by fishing method for period 1983/4 – 98/9. The dashed lines represent average catches from 1983/4 to 1998/9. HL handline, LL longline, HN haulnet.

The longline catch remained relatively stable from 75 – 85 tonnes between 1983/84 and 1989/90 after which it rose to a peak of 110.5 tonnes in 1992/93 (Fig. 2.5). However, this catch decreased by nearly 50% to 59.7 tonnes in 1998/9, to the lowest level recorded since 1982/3 when this sector fully developed. Longline fishers generally use similar sized vessels to those used in the handline fishery. Lines are usually set with 50 - 100 hooks and up to 400 hooks may be set per day.

The most significant longline fishery exists in northern Spencer Gulf between Whyalla and Port Pirie and north beyond Pt Lowly. Longlines are set in late afternoon and retrieved the following morning. In contrast to the predominantly summer handline fishery of northern Spencer Gulf, the longline fishery occurs from autumn through to late spring. Average targeted effort over the last 13 years shows two seasonal peaks: the first from April - June and a greater peak from August to September. Effort then declines and is relatively low from November to February. Longline fishing is inhibited in summer by the arrival of trumpeters (*Pelates octolineatus*), rays and sharks on the fishing grounds. Longlines are required to be attended by fishers when set. However, a general exemption to this requirement exists in waters of northern Spencer Gulf (north of latitude 34°S).

The haul net fishery produced a maximum of 37.3 tonnes in 1983/84 and has declined to zero since the use of this gear was prohibited for taking snapper in 1993 (Fig. 2.5). Other methods used to take snapper included fish traps, large mesh nets and droplines. While they were relatively important in some offshore waters, the total catch from these methods has not exceeded 37.2 tonnes and has generally been less than 20 tonnes (Fig. 2.5).

Catches are not distributed evenly throughout the State, with Spencer Gulf and particularly northern Spencer Gulf producing the largest proportion of the commercial catch (Table 2.2).

Table 2.2 Regional catches and percentage of annual catch (all methods combined) from 1983/4 – 1998/9

YEAR		83/4	84/5	85/6	86/7	87/8	88/9	89/90	90/1	91/2	92/3	93/4	94/5	95/6	96/7	97/8	98/9
REGION																	
NSG	Tonnes	222.2	220.1	236.7	208.1	169.2	218.6	243.5	271.3	256.5	255.7	213.1	154.3	224.3	197.9	256.2	278.4
	%	47.7	46.7	52.0	51.4	50.8	48.9	57.5	59.4	58.7	66.3	67.0	69.1	73.3	64.8	65.1	62.5
SSG	Tonnes	115.0	107.5	90.0	92.5	60.4	124.7	95.4	114.9	97.2	69.7	41.4	27.7	45.7	53.7	82.0	110.0
	%	24.7	22.8	19.8	22.8	18.1	27.9	22.5	25.2	22.2	18.1	13.0	12.4	14.9	17.6	20.8	24.7
NGSV	Tonnes	28.2	34.0	22.1	13.1	12.0	12.2	10.7	7.9	18.2	12.9	14.1	17.5	9.0	14.8	16.3	18.0
	%	6.0	7.2	4.9	3.2	3.6	2.7	2.5	1.7	4.2	3.3	4.4	7.8	2.9	4.8	4.1	4.0
SGSV	Tonnes	75.5	85.1	76.7	53.3	47.9	49.7	45.0	42.4	35.6	28.4	23.3	10.9	13.6	22.0	20.9	18.1
	%	16.2	18.1	16.9	13.2	14.4	11.1	10.6	9.3	8.1	7.4	7.3	4.9	4.4	7.2	5.3	4.1
WC	Tonnes	15.0	15.7	18.0	22.8	25.1	30.8	22.0	16.0	25.4	16.6	23.4	9.7	7.6	11.4	12.7	16.4
	%	3.2	3.3	4.0	5.6	7.5	6.9	5.2	3.5	5.8	4.3	7.4	4.3	2.5	3.7	3.2	3.7
OTHER	Tonnes	9.6	8.6	11.5	15.0	18.6	11.0	6.7	4.3	4.3	2.3	2.8	3.1	5.9	5.6	5.5	4.4
	%	2.1	1.8	2.5	3.7	5.6	2.5	1.6	1.0	1.0	0.6	0.9	1.4	1.9	1.8	1.4	1.0
TOTAL		465.5	471.0	455.1	404.8	333.2	447.0	423.3	456.8	437.2	385.5	318.2	223.2	306.1	305.3	393.6	447.3

2.2.3 Recreational Fishery

The recreational fishery for snapper also extends throughout most State coastal waters. Recreational fishers generally fish from boats and exclusively use lines (either handlines or rod and lines), although snapper are occasionally caught as by-catch in rock lobster pots. The recreational boat fishery was extensively surveyed between April 1994 and March 1995 (McGlennon and Kinloch 1997), using a survey method known colloquially as the bus-route method (Robson and Jones 1989; Jones et al. 1990). The spatial coverage of the survey included the waters of Gulf St Vincent, Spencer Gulf and those of the western coast of Eyre Peninsula and therefore included all of the main snapper fishing grounds. The study area was divided into three regions - Gulf St Vincent (including Investigator Strait), Spencer Gulf and West Coast - which were each surveyed for 12 months. The results were then summed across regions to provide an estimate of annual catch and effort for the recreational boat fishery.

The survey was designed to provide a comprehensive description of the overall recreational fishery, rather than specific results for snapper, and some of the night fishing for snapper was not sampled. However, the survey provided the most comprehensive information available at the time of writing.

Recreational anglers targeted snapper for 15%, 6%, 3% and 2% of their fishing time in NSG, SSG, Gulf St Vincent and West Coast waters respectively, for an annual targeted fishing effort estimated at 11,232 boatdays. This equated to 5.7% of the overall recreational fishing effort of 196,900 boatdays (McGlennon and Kinloch 1997). The length frequency distribution of snapper harvested by anglers was similar to that from commercial landings in the same area suggesting that both sectors target the same snapper populations.

The total recreational harvest was estimated at 3,071 snapper or 10.8 tonnes for Gulf St Vincent, and 20,372 snapper or 36.2 tonnes for Spencer Gulf. The spatial breakdown of this harvest is shown in Fig. 2.6, along with a comparison with the commercial catch during the same period. The recreational share (tonnes) of the snapper total catch was 26.9% for Gulf St Vincent, 12.8% for Spencer Gulf and 14.5% for the State.

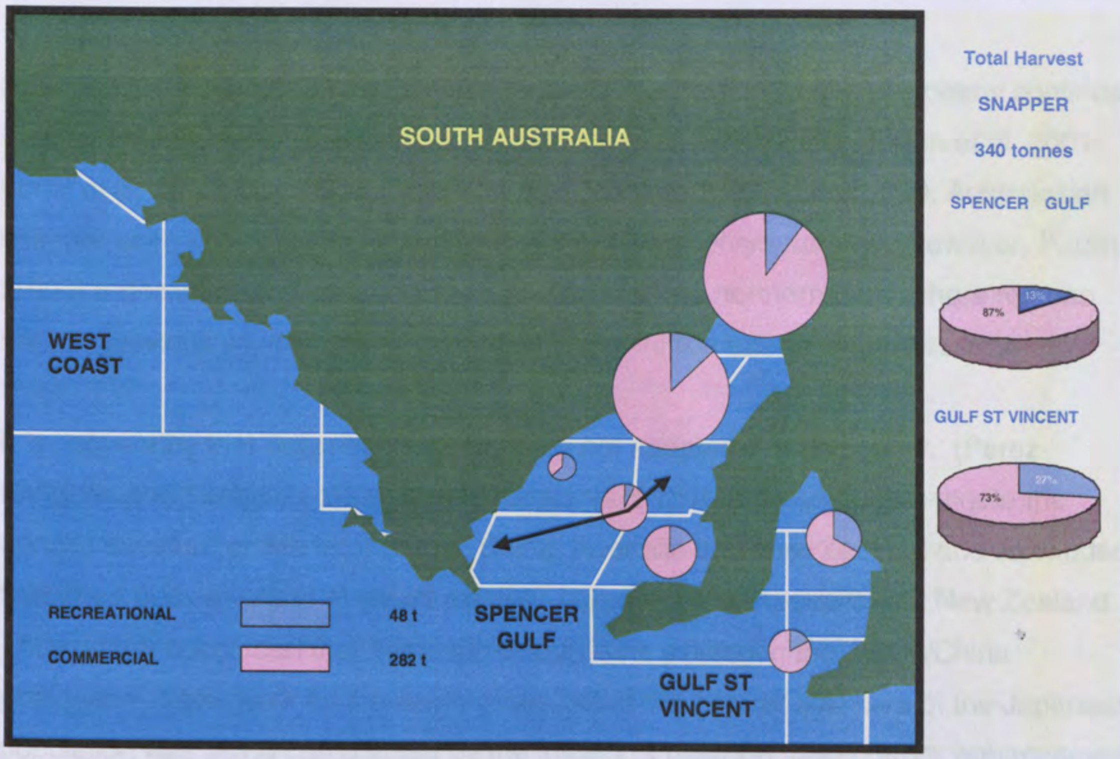


Fig. 2.6 Spatial representation of the commercial and recreational catch of snapper (Gulf St Vincent April 1994 – March 1995; remaining waters April 1995 – March 1996) (from data in (McGlennon and Kinloch 1997). The area of the circles is proportional to the overall catch in that region.

There were also a number of annual recreational fishing competitions, some of which are focused on snapper (primarily the Whyalla and Streaky Bay competitions). The Whyalla competition is the largest, attracting nearly 1,000 competitors from South Australia and interstate for a three day period in late January. Harvest levels of these competitions were not monitored.

2.3 Summary of the biology of *Pagrus auratus*

A bibliography compiled by Larry Paul (National Institute of Water and Atmospheric Research, New Zealand) in 1993 listed 237 Australian, New Zealand and Japanese papers relating to snapper (Ferrell and Morison 1993). The following overview places particular emphasis on the aspects of the life history of the species that are relevant to this study and so only includes a small portion of this literature. The overview generally excludes, for example, the numerous studies related to the culture of snapper.

2.3.1 Taxonomy

Sparidae are a numerous and diverse family of marine fish whose phylogeny continues to attract much research effort (Garrido-Ramos et al. 1999; De la Herran et al. 2001; Orrell et al. 2002; Day 2002; Carpenter and Johnson 2002). Until 1990, Australasian snapper were known by the scientific name of *Chrysophrys auratus.* However, Paulin (1990) redescribed the species in conjunction with the northern hemisphere red sea bream (previously known as *Pagrus major*) to unite the two as *Pagrus auratus.*

It is noteworthy that Japanese research has not adopted this taxonomy. (Perez-Enriquez and Taniguchi 1999) used microsatellite DNA markers to investigate the genetic structure of fish from Japan, China, Australia and New Zealand and concluded that three populations of *P. major* existed – Japan/China, Australia and New Zealand. They further concluded that three sub-populations existed in the Japan/China population. Later work by the same group noted the genetic structure of the Japanese population was being confounded by the impact of hatchery based stock enhancement (Perez-Enriquez et al. 2001). Separate Japanese genetic results concluded that *P.auratus* and *P. major* separated 2 – 6 million years ago and that their relationship is at the sub-species level – *P.auratus auratus* for the southern hemisphere populations and *P. auratus major* for the northern hemisphere (Tabata 2000).

For the purposes of this study, the findings of Paulin (1990) are followed with *P. auratus* used for northern and southern hemisphere populations. It is considered to be a widely distributed western Pacific species with a number of reproductively isolated populations throughout a discontinuous range (Francis et al. 1992).

2.3.2 Reproduction and early life history

The gonads of *P.auratus* are sexually undifferentiated in their first year but then develop into ovaries during their second year (Francis and Pankhurst 1988; Matsuyama et al. 1988). During the following 1-2 years, about 50% of the immature females change sex to males and by age 5+ are fully differentiated into either males or females. This development pattern has been described as juvenile sex inversion and functional gonochorism (Francis and Pankhurst 1988). Snapper first become reproductively mature at fork lengths (LCF) of approximately 23 – 28 cm in Australia and New Zealand (Crossland 1977b; Jones et al. 1990), while Matsuyama et al. (1987)

reported both male and female maturity was first evident at 20 – 22 cm LCF with 50% maturity at 28 – 30 cm LCF in Japan.

P.auratus are serial daily spawners (Crossland 1977b; Matsuyama et al. 1988; Scott et al. 1993) i.e. each individual female can spawn on a daily basis for an extended period of time. Spawning in the New Zealand populations extends for 3.5 – 5 months within the period of October to January/February (Crossland 1977b; Scott and Pankhurst 1992), and a similar duration and period in South Australia (Jones 1981). The duration appears to vary between years and may depend on water temperature and other weather variables (Scott and Pankhurst 1992).

Snapper eggs are approximately 0.85 – 1.0 mm in diameter with a single oil droplet (approximately 200 μm diameter), unsegmented yolk and a narrow perivitelline space (Cassie 1956; Crossland 1980; Fukuhara 1985). The eggs are pelagic and hatch in about 36 hours at 21°C. The larvae are approximately 2 mm total length at hatch and are also pelagic during their early development (Fukuhara 1985). They depend on endogenous metabolism from the yolk for the first 2-3 days after which external feeding commences. Larvae grow to about 10mm in the first month at which time they settle out as demersal juveniles (Tanaka 1985). Snapper larvae have been recorded in bays and inlets in Western Australia, Victoria and New South Wales, as well as coastal waters near Sydney, New South Wales (studies reported in Miskiewicz and Neira 1998).

Recruitment is highly variable in New Zealand populations, with relative numbers varying 17 fold over a seven year period (Francis 1993; Davies and Walsh 1995; Walsh et al. 1995). This interannual variability is highly correlated with water temperature in some regions: in spring (Horn 1986), autumn (Francis 1993) or at the time of spawning (Maunder and Watters 2003). Japanese populations have also shown variable recruitment at levels of 7 and 10 fold variation over 3 and 5 year time periods (Matsumiya et al. 1980; Kojima 1981). Juvenile snapper are believed to prefer sandy/silty seabeds in about 10m depth (Tanaka 1985)).

2.3.3 Age

Snapper are relatively long-lived with ages estimated of > 20 years in South Australia (Jones et al. 1990) and of 30 – 60 years in New Zealand (Horn 1986; Francis et al. 1992).

2.3.4 Diet

Tanaka (1985) recorded diatoms, dinoflagellates, invertebrate eggs, copepods and appendicularians in the diet of pelagic larvae, and copepods, amphipods, mysids, fish eggs, polychaetes and Sagittoidea in metamorphosed juveniles in Shijiki Bay, Japan.

Adult snapper are considered to be opportunistic benthic feeders in South Australia (Jones 1981). Their diet changes from predominantly prawns in small fish to crabs and mussels in larger fish in northern gulf waters, while also including scallops and echinoderms in southern Gulf and shelf waters. Godfriaux (1974) found that size of fish affected diet as did time of day, depth and sampling area but sex did not. The main food groups were crustaceans, polychaetes, molluscs, echinoderms and teleosts.

Chapter 3. Length frequency distributions and age composition of the commercial catch of *Pagrus auratus* in northern Spencer Gulf

3.1 Introduction

An accurate estimate of the age composition makes a significant contribution towards an understanding of fish population dynamics. The collection and interpretation of length, age and weight information makes it possible to follow yearclasses through time and to understand growth, interpret population changes over time and to calculate age and sex specific estimates of population parameters (Quinn and Deriso 1999). Monitoring age composition becomes increasingly important where inter-annual recruitment is variable, where fluctuations occur in population biomass, growth rates, natural mortality and fecundity (Sissenwine et al 1988). Length frequency analyses of the northern Spencer Gulf snapper catch have been done irregularly since 1977/78 (Jones 1981; Jones 1984a; Jones et al. 1990) and have demonstrated changes in the length composition of catches between fishing methods, seasons and years - indicating a relatively complex dynamic at work occurring at several different time scales.

Snapper is a relatively long-lived fish species with estimates of maximum age of 20 – 60 years at different places (Horn 1986; Jones et al. 1990; Francis et al. 1992). In long-lived species, length frequency distributions mask information about single yearclasses due to the overlap of the sizes of fish from different age classes, particularly for older fishes. Establishing an age structure can therefore lead to a more powerful understanding of demographic processes throughout the life history of the species. Previous ageing studies of South Australian snapper have relied on direct ageing from periodic marks on scales (Jones 1981; Jones 1984a). However, comparative studies between scales and sagittal otoliths for this species have shown the potential for under-estimates of age in older snapper using scales (Paul 1976). It has thus been recommended that otoliths be used for direct ageing purposes of snapper (Francis et al. 1992). This study, therefore, developed an otolith ageing methodology based on the microstructure of the otoliths for South Australian snapper for the first time.

The study used length data and otolith samples from two time periods, i.e. 1991 and 1994/5. The otolith and scale samples from 1991 were collected and archived by the author and have been used to develop age-length keys with data from a market measuring program conducted by Dr Keith Jones (Marine Scalefish Fishery Unit, South Australian Research and Development Institute) at the same time (McGlennon et al. 2000). The later otolith samples and length frequency data were collected concurrently from July 1994 to June 1995 by the author.

Specifically, this study used:

1) market measuring information to determine the length frequency distributions of snapper caught seasonally by handline and longline in 1991 and 1994/95;
2) otolith samples to
    a) establish a reliable ageing procedure by
        i) analysing the bias and precision of multiple readings
        ii) determining the timing of annulus formation
        iii) comparing the results of ageing snapper with scales
    b) assess the utility of otolith weight as a proxy for age
3) the information obtained from market measuring and ageing to:
        i) quantify catch-at-age of the handline and longline sectors of the commercial fishery
        ii) interpret changes in the length and age structures between sampling years.

3.2 Methods

3.2.1 Market measuring

Market measuring programs for snapper were done weekly from January to December 1991 (McGlennon et al. 2000) and fortnightly from July 1994 to June 1995 (referred to as 1994 in this paper) at SAFCOL, the major Adelaide fish market. There was also some opportunistic sampling at processing plants in regional centres. Fish arrived by transport at the SAFCOL market from approximately 0530 hours, selling commenced at 0700 hours (0630 Fridays) and so sampling was only possible between these hours. Where possible, all snapper were measured (caudal fork length (LCF) to the centimetre below) from each individual landing. Snapper are landed over a large size range, from

32 cm LCF (≅ legal minimum length of 38 cm total length) to 96 cm LCF, and are generally graded by fishers when packed into fish bins. When insufficient time was available to measure all snapper within a landing, a random sample of fish from each size range was measured and the data were multiplied to equal the number of bins of that size fish present in the landing.

For the length frequency analyses, the data were stratified by fishing method (handline and longline) and season (Jan-Mar, Apr-Jun, Jul-Sept, Oct-Dec). The computational procedure followed (Davies and Walsh 1995). First, the proportion at length was calculated for each stratum. The number of snapper landed in each stratum was then estimated by:

1) calculating the mean weight of fish landed using a) the length-weight relationship for South Australian snapper (weight (kg) = 1.56×10^{-5} * LCF (cm) $^{3.0}$ (Jones et al. 1990) and b) the proportion at length estimates and
2) dividing total reported catch weight (derived from monthly catch and effort returns provided by commercial fishers) by the estimated mean fish weight.

Stratum length frequencies were converted to an annual length frequency for each gear type by weighting the stratum proportions at length by the number of snapper landed in each season.

3.2.2 Ageing and catch at age

3.2.2.1 Sample collection and processing

The use of annuli in otoliths for assigning fish to an appropriate age class is dependent on three factors: known periodicity of formation; the ability to interpret annuli precisely; and knowledge of the timing of annulus formation. The periodicity of formation has been validated as annual in *P. auratus* otoliths for 0+ and 1+ fish in eastern Australia (Ferrell et al. 1992) and for fish up to 30 years old in New Zealand (Francis et al. 1992). No further validation was done during this study.

To investigate both reading precision and the timing of annulus formation, sagittal otoliths were extracted from a random selection of snapper, proportional to number at length, during the measuring programs and during other snapper research activities. Snapper collected during research activities included fish less than the legal minimum length. The snapper are landed by commercial fishermen in gilled and gutted condition, i.e. with gills and viscera removed. The otoliths were extracted by making two incisions on the ventral surface of the first vertebra, approximately 1 centimetre apart (variable with fish size), and to a depth of 1-2 cm (again variable with fish size). The bone between these incisions was then removed exposed the sagittae which were removed using forceps. They were stored in plastic bags and labelled with sequential numbers, the sampling date and fish length (fork length LCF in cms).

The otoliths were cleaned ultasonically in the laboratory and air-dried for 24 hours. Each otolith was then weighed to the nearest 0.0001g using a Mettler AE 200 analytical balance. The whole otolith was measured to the nearest 0.1 mm with a micrometer 1) from anterior tip to posterior tip (length) and 2) transversely from the ventral to the dorsal margins through the primordium at 90^0 to the length measurement (width). One otolith from each fish was embedded in polyester resin with a number of otoliths aligned by their primordia. After setting, the resin blocks were clamped in a Struers Accutom 2 saw and 3 - 4 cuts were made transversely through each row of otoliths using a diamond tipped blade. The cuts spanned the primordia of the otoliths in each row and produced otolith sections of 300-500 μms thickness. The 2 – 3 sections for each set of otoliths were then glued to a microscope slide for later reading.

Scale samples (n = 422) were collected from beneath the mid-point of the pectoral fin from a sub-sample of fish from the 1991 sample. Scale rings were interpreted independently by two readers, assigned an index of readability (0 – 4) (Table 3.1) and an agreed ring number determined for scales with a readability > 2. A further sample of scales (n = 48) was read from older fish from the 1994 sample. The scale reading process followed descriptions by (Paul 1976) and was made using a micro-fiche reader.

Table 3.1 Readability categories for snapper scale and otolith readings

Readability	Characteristics
0	Internal structure impossible to interpret
1	Annuli and/or margin very difficult to interpret with significant uncertainty remaining in the count and/or margin
2	Annuli and/or margin moderately difficult to interpret with some uncertainty remaining in the count and/or margin
3	Annuli and margin generally clear with any uncertainty within the counting region resolvable from other regions of the otolith
4	Annuli and margin clear with no region providing interpretation uncertainty

3.2.2.2 Interpretation and analysis

The utility of otoliths for reliable snapper ageing was first evaluated by exploring the bias and precision associated with multiple readings. The otoliths were read using a binocular microscope at magnifications of x16 – 40 using transmitted light. Initial readings were done independently by two readers without knowledge of capture date and length of fish. For each sample, the multiple sections of each otolith were scrutinised to locate the one which most clearly showed the primordium. Counts were made of opaque annuli, from the primodium along a line to the margin on the proximal side of the dorsal tip (Fig. 3.1). In older fish the annuli were often better counted along the dorsal side of the sulcus (Fig. 3.2).

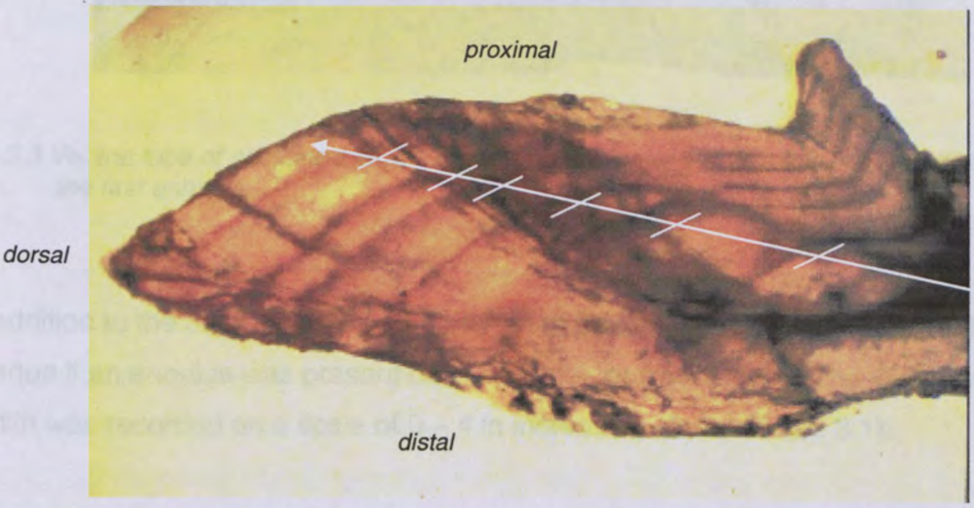


Fig. 3.1 Sectioned sagittal otolith of a 6 year old P. auratus showing counts of annuli from the primordium to the dorso-proximal margin.

Fig. 3.2 Proximal margin of a 26 year old P. auratus otolith. *Counts of annuli for older snapper were generally made along the ventral margin of the sulcus (white line).*

The first annulus was identified using the inflection of the "Francis line" on the ventral lobe (Francis 1994) (Fig. 3.3).

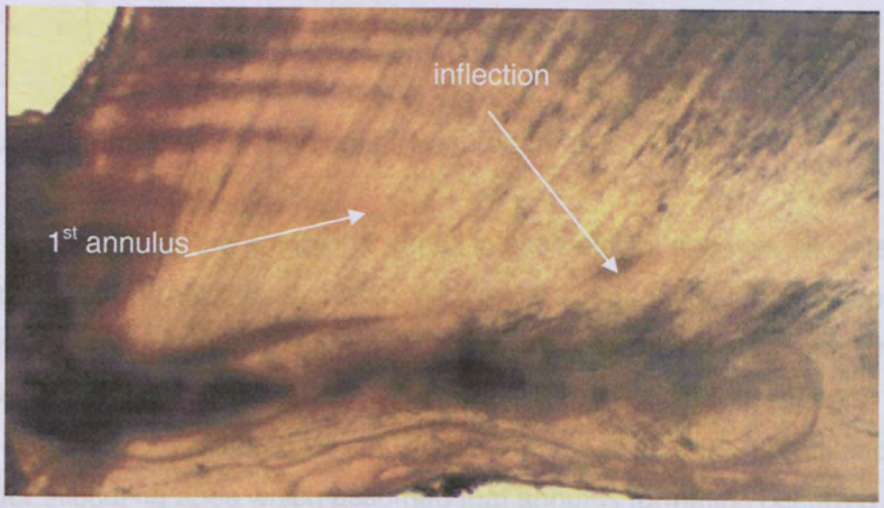


Fig 3.3 Ventral lobe of sectioned otolith showing inflection of the "Francis line" used to identify the first annulus.

In addition to the count of annuli, the margin of the otolith was recorded as either opaque if an annulus was present on the margin, or translucent. The readability of the otolith was recorded on a scale of 0 – 4 in increasing clarity (Table 3.1).

Following the independent readings, the data were compared. Readings of otoliths where readability was > 2 and where the counts of annuli and margins agreed were accepted. Where disagreements on counts or edgetype occurred, the otoliths were re-read jointly and agreement reached, or else the otolith was discarded.

The bias in initial counts of annuli between readers was evaluated by deriving an age bias plot for each sample. The age bias plot graphically compared counts of annuli and allowed visual detection of differences or biases as a systematic deviation of data from a 1:1 equivalence line (Campana et al. 1995). The results were portrayed as a mean and 95% confidence interval of counts from reader two for fish from a single count group (e.g. 4, 5, 6, ..., 34) from reader one.

The precision of independent counts was evaluated by calculating the coefficient of variation (CV) for counts from individual fish and averaging the CV within each count group (Campana et al. 1995). The CV for individual fish was calculated by

$$\left(\frac{\sqrt{\left(Count_i - \overline{count}\right)^2 + \left(Count_j - \overline{count}\right)^2}}{\overline{count}} \right) * 100 \qquad (3.1)$$

where $count_i$ is from reader 1, and $count_j$ from reader 2.

Following agreement on the number of annuli in each otolith, age was allocated using a similar approach to (Francis et al. 1992). A birth date of January 1st has been used for New Zealand snapper (Paul 1976; Francis et al. 1992) which spawn at similar times to those in South Australia (Crossland 1977b; Jones 1981; Scott and Pankhurst 1992). This date was therefore adopted for this study. Francis et al. (1992) produced an algorithm for allocating ages which assumed that annulus formation occurred during winter, but was not readily observed until additional material was laid down in late spring for juveniles and summer for adults. This algorithm proved generally applicable for South Australian snapper although some differences were noted for fish older than 5+. To account for this difference, the marginal and penultimate increments of all samples with translucent margins collected between November and February were measured and compared (by %) to determine whether the last ring had been laid down recently or in the previous year. Narrow marginal increments (i.e. <33% of the penultimate increment) were deemed to lay outside an annulus which had been laid down in the preceeding spring, whereas wider marginal increments reflected annuli laid down 12 months earlier.

An age-length key was constructed for each sample and catch at age calculated using the weighted annual length frequency distributions for each gear type. Proportion at age calculations again followed Davies and Walsh (1995) and calculation of the coefficient of variation for a proportional sample followed (Southward 1976).

3.2.3 Relationship between otolith size and age

Francis (1992) examined the relationship between otolith morphometrics (four different linear measurements and weight) and age for New Zealand snapper, and found that the scatter of measurements at each estimated age precluded the use of any of these measurements as a precise predictor of age. He noted, however, that the relationship between otolith weight and estimated age was "nearly linear" and showed much less scatter. His sample of 406 otoliths contained only 4 fish with ages > 20 years and yet variability of otolith weight between individual fish is likely to increase as age increases. I have used the length, width and weight of 421 otoliths from the 1994/95 sample to examine their relationships with estimated age. Initial evaluation used scatterplots of each set of data and, for the age – weight relationship, a linear regression was calculated.

3.2.4 Relative year class strength and temperature

An exploratory investigation was made between observed year class strength and temperature. Air temperature at Port Pirie was used as a proxy for water temperature as time series water temperature data were not available for any location in northern Spencer Gulf. Mean maximum air temperatures from 1970 to 1991 were obtained from the South Australian Yearbooks (Australian Bureau of Statistics, Vols. 1971 – 1992) and plotted for the quarters January - March, April - June, July - September and October - December. These temperatures were then qualitatively compared with yearclass strengths observed from the catch at age results.

3.3 Results

3.3.1 Length frequency distributions

A total of 6,427 snapper from 203 landings and 1,867 snapper from 56 landings were measured during market visits in 1991 and 1994/95 respectively (Table 3.2). Supply of snapper to the processors was often sporadic in 1994/95 and many trips resulted in few or no fish being located, particularly for longline caught fish. It should be noted that the sampling period in 1994/95 recorded the lowest commercial snapper catches in 30 years (Chapter 2), whilst the commercial catch in 1991 was at relatively high levels.

Table 3.2 Number and weight of snapper measured, and number of otoliths collected, during market measuring programs in 1991 and 1994 compared to the number and weight of snapper landed seasonally in the commercial fishery. HL, handline; LL, longline.

Method / year	Season	Total caught (nos)	Number measured	%	Total wt caught (t)	Weight measured (t)	%	No. otoliths (HL + LL)
HL 1991	Summer	11,539	2,356	20.4	41.2	8.4	20.4	204
	Autumn	13,585	1,422	10.5	29.7	3.1	10.5	34
	Winter	4,055	447	11.0	10.8	1.2	11.0	91
	Spring	23,324	1,297	5.6	105.9	5.9	5.6	183
	Total	52,503	5,522	10.5	187.6	18.6	9.9	512
LL 1991	Summer	808	262	32.4	6.9	2.2	32.4	
	Autumn	1,807	373	20.6	14.5	3.0	20.6	
	Winter	1,744	270	15.5	14.0	2.2	15.5	
	Spring	575	266	46.3	4.8	2.2	46.3	
	Total	4,934	905	18.3	40.2	9.6	23.9	
HL 1994	Summer	20,861	889	4.3	34.7	1.5	4.3	135
	Autumn	23,666	184	0.8	24.3	0.2	0.8	210
	Winter	6,646	179	2.7	12.6	0.3	2.7	61
	Spring	13,274	244	1.8	28.8	0.5	1.8	126
	Total	64,147	1,496	2.3	100.4	2.5	2.5	532
LL 1994	Summer	1,372	47	3.4	12.1	0.4	3.4	
	Autumn	2,039	100	4.9	18.1	0.9	4.9	
	Winter	1,480	224	15.1	14.6	2.2	15.1	
	Spring	1,561	18	1.2	8.8	0.1	1.2	
	Total	6,452	371	5.8	53.7	3.6	6.7	

The handline catch in 1991 showed significant seasonal changes in length frequencies (Fig. 3.4). The size distribution in January-March was bi-modal with equivalent numbers of small and large fish. The proportion of the larger fish decreased significantly from April to September but returned strongly from October to December when they dominated the catch. Such seasonal changes were not as pronounced in 1994 although the relatively few larger fish in the sample were only evident from October to March (Fig 3.4). The longline catch showed no seasonal patterns in size distribution in either sampling year.

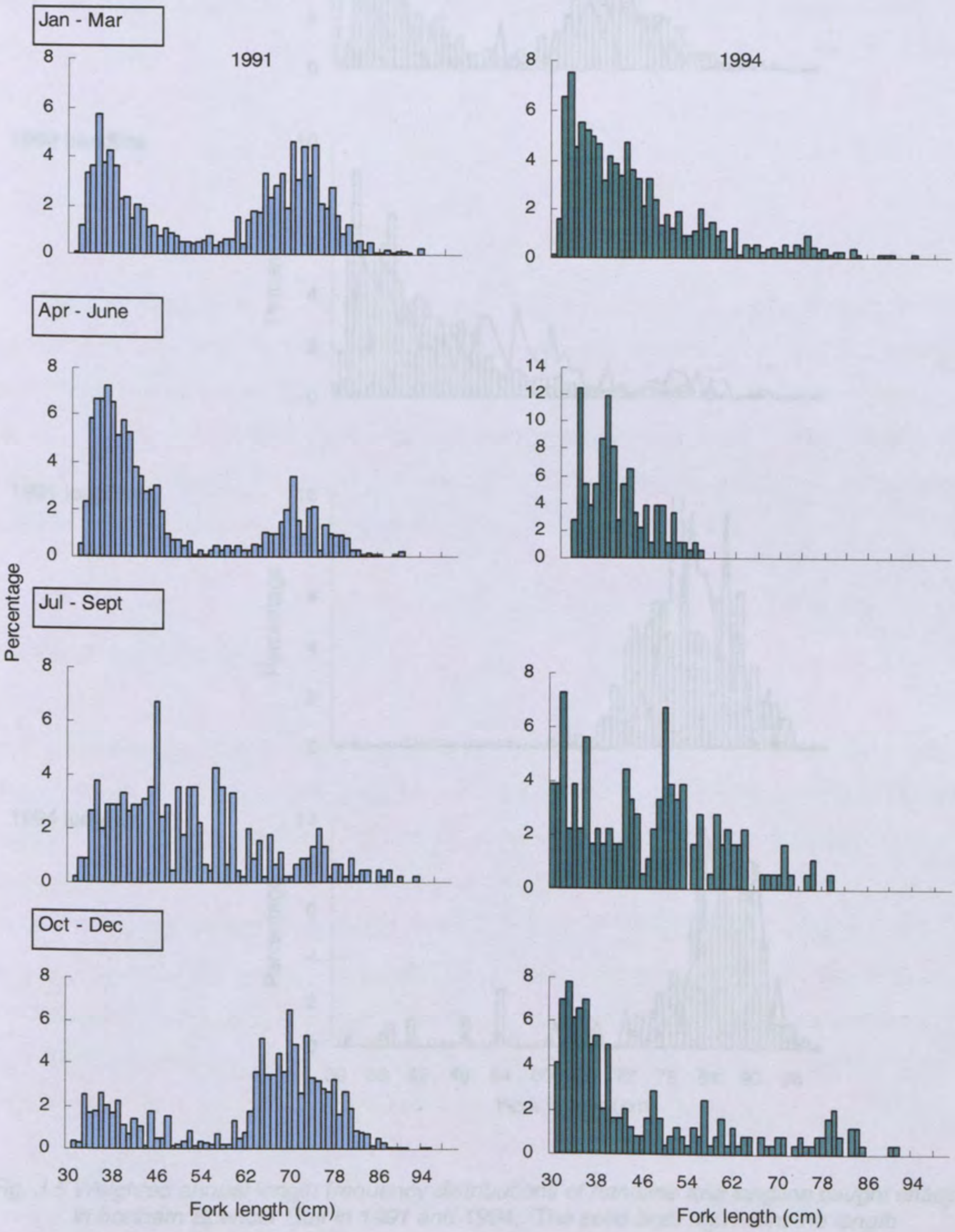


Fig. 3.4 Seasonal length frequencies for the snapper handline catch of northern Spencer Gulf in 1991 and 1994.

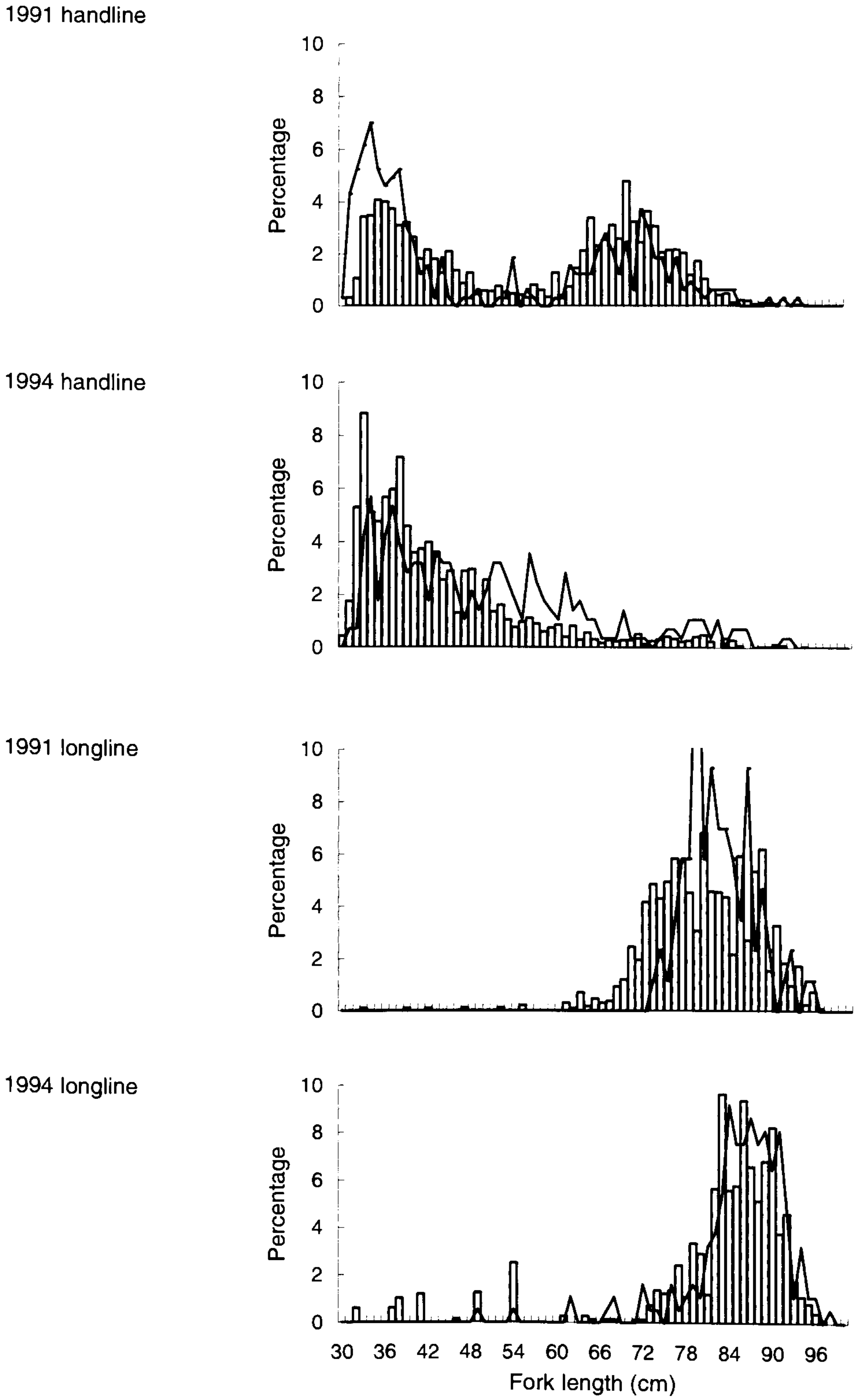


Fig. 3.5 Weighted annual length frequency distributions of handline and longline caught snapper in northern Spencer Gulf in 1991 and 1994. The solid lines represent the length frequency distribution of the fish sampled for otoliths

The annual length frequency distribution (seasonal distributions weighted by stratum landings) for the handline sector was markedly different between 1991 and 1994 (Fig. 3.5). The 1991 distribution was bi-modal with peaks at about 35 cm and 70 cm LCF, whereas the 1994 distribution was dominated by small fish (< 45 cm LCF) with relatively few large fish present. The length frequency distribution of longline fish changed less between 1991 and 1994 but in each case primarily included fish that were significantly larger than in the handline fishery (Fig. 3.5). The average size of longline caught fish was approximately 80 - 90 cm LCF and an average weight of 8.2 kg.

3.3.2 Ageing

The initial number of otoliths collected in the 1991 sample was 512 (Table 3.2). After the interpretative process, 382 (74.6%) counts were agreed and, of these, 322 were taken from fish within the size range of the landings of the commercial fishery and constituted the sample from which the age-length key was derived. For the 1994 sample, the initial sample size, agreed counts and final sample size used for the age-length key were 532, 468 (88.0%) and 423 respectively.

3.3.2.1 Bias and precision

No systematic bias was evident in dual readings of otoliths from either 1991 or 1994 (Figs 3.6a, b). Initial counts of annuli from the second reader closely followed Reader 1 in both samples, with small confidence intervals in most cases. The greatest discrepancy occurred for the oldest fish from the 1991 sample where Reader 2 differed by four annuli. However, in the later sample, fish older than 25 years were counted within ±2 annuli in all cases. The precision of counts of annuli was high. The mean coefficient of variation (CV) for each annulus count group in both samples was less than 10% and was generally less than 6% (Figs 3.6a, b). The overall mean CV was 2.61% and 1.94% for the 1991 and 1994 samples respectively.

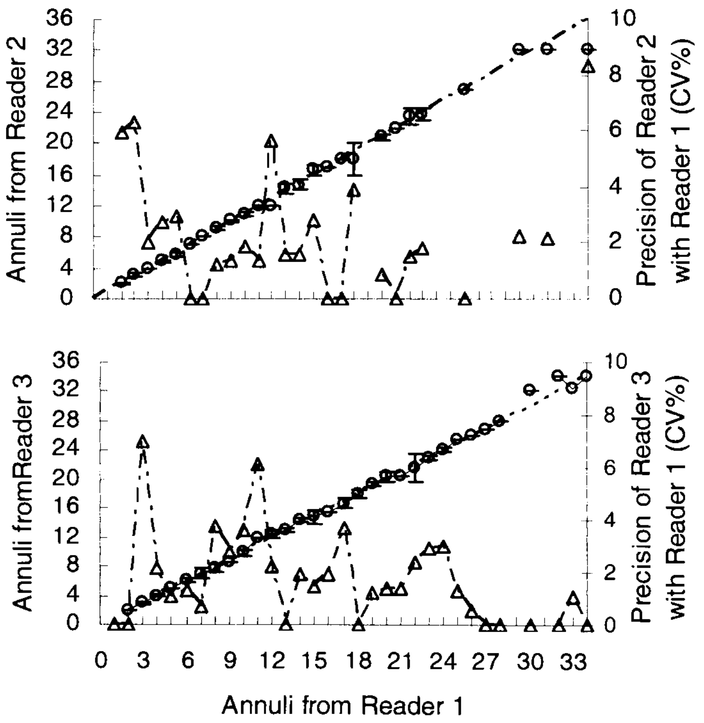


Fig. 3.6 Bias and precision in dual counts of otolith annuli from snapper from northern Spencer Gulf in top) 1991 and bottom) 1994/5. The count data (o) are mean values assigned by Reader 2 for all fish assigned a single value by Reader 1, and are plotted against a 1:1 equivalence line. The error bars are 95% confidence intervals. The precision of counts of Reader 2 with Reader 1 (D) is the mean coefficient of variation (CV) for each individual fish per age.

3.3.2.2 Timing of annulus formation

The formation of annuli (defined by opaque otolith margins) was recorded to occur from November to February (Fig. 3.7). No otoliths were collected in October and so it cannot be stated whether annulus formation commences in this month. For fish 5 years old or less, annulus formation was predominantly recorded in November and December, with only one opaque margin recorded from February. However, marginal annuli were recorded for fish from 5 – 11 years in November, January and February. Opaque margins in fish 12^+ and older were most commonly observed in January (18 out of a sample of 40 fish recaptured in January), with one opaque margin recorded from two fish captured in February, but none in November or December (from 18 fish captured in those two months).

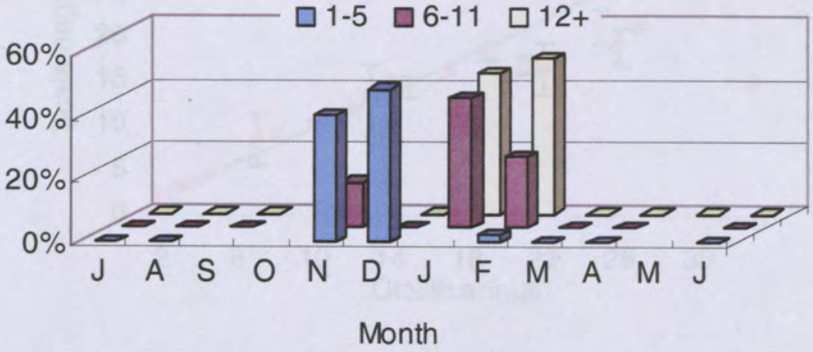


Fig. 3.7 Percentage occurrence of opaque otolith margins for snapper from northern Spencer Gulf (ages 1-5, 6-11 and 12+) for combined 1991 and 1994 samples.

3.3.2.3 Otolith v scale counts

The comparison of counts of scale rings and otolith annuli clearly showed an age-dependent bias, with scale ring counts under-estimating ages of fish older than 18 years relative to counts from otoliths (Fig. 3.8). The comparison for fish up to 19 years (annuli counts) showed general agreement with only 5 (5%) counts differing by more than ± 1. However, all scale ring counts for fish > 19 years under-estimated otolith annulus counts by 3 – 18 years. There was also an age-dependent difference in readability between scales and otoliths (Fig. 3.9). Scale readabilities of 1 or 2, which were routinely discarded due to significant uncertainties, increased from about 20% in 1 – 5 year old fish to 52% in fish > 12 years, whereas the percentage was relatively unchanged at about 6 – 8% for otoliths.

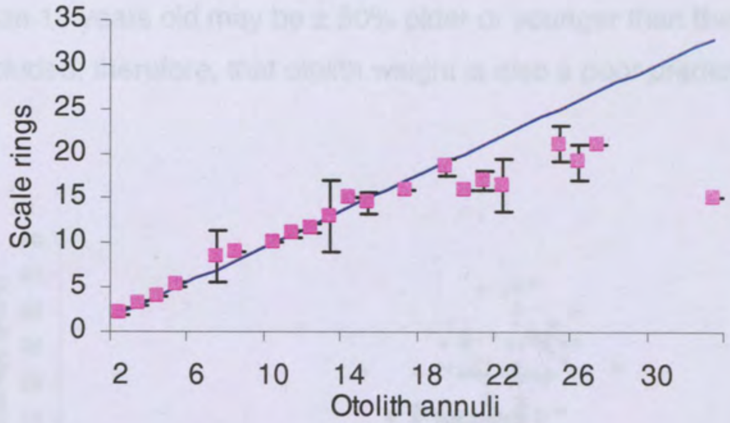


Fig. 3.8 Comparison of scale ring and otolith annulus counts from 124 snapper with otolith determined ages of 2 – 33. Error bars are 95% confidence intervals.

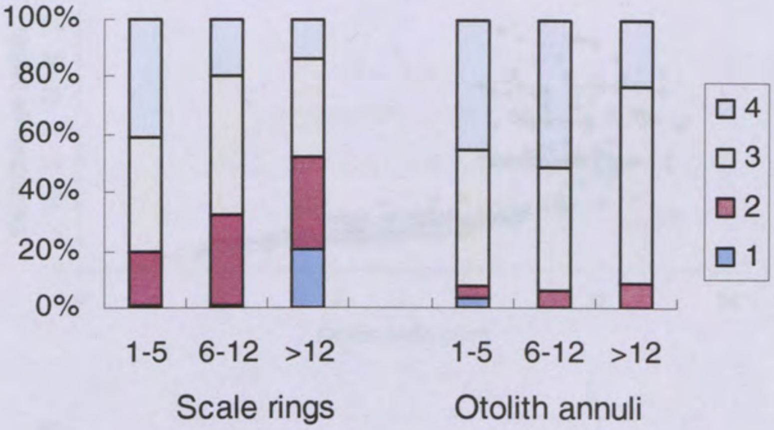


Fig. 3.9 Comparative readability of scales (n = 461) and otoliths (n = 1,013) for different age snapper, with readability increasing from 1 – 4.

3.3.3 Otolith morphometrics

The relationships between estimated age and otolith length and width were non-linear with a significant slowdown in growth in both directions after about 10 years of age (Figs. 3.10 & 3.11). There was a high degree of scatter after that age and, in terms of use as a proxy for age, both measurements offered little potential. The relationship between age and otolith weight was more closely linear (Fig. 3.12). The regression of estimated age and otolith weight produced a significant relationship ($P < 0.000$) with a high level of fit ($R^2 = 0.89$) (Fig. 3.10). However, the residuals showed that individual age estimates may be ≈ ± 10 years from the predicted age for older fish (Fig. 3.11). Even fish less than 10 years old may be ± 50% older or younger than their predicted age. It was concluded, therefore, that otolith weight is also a poor predictor of age in this species.

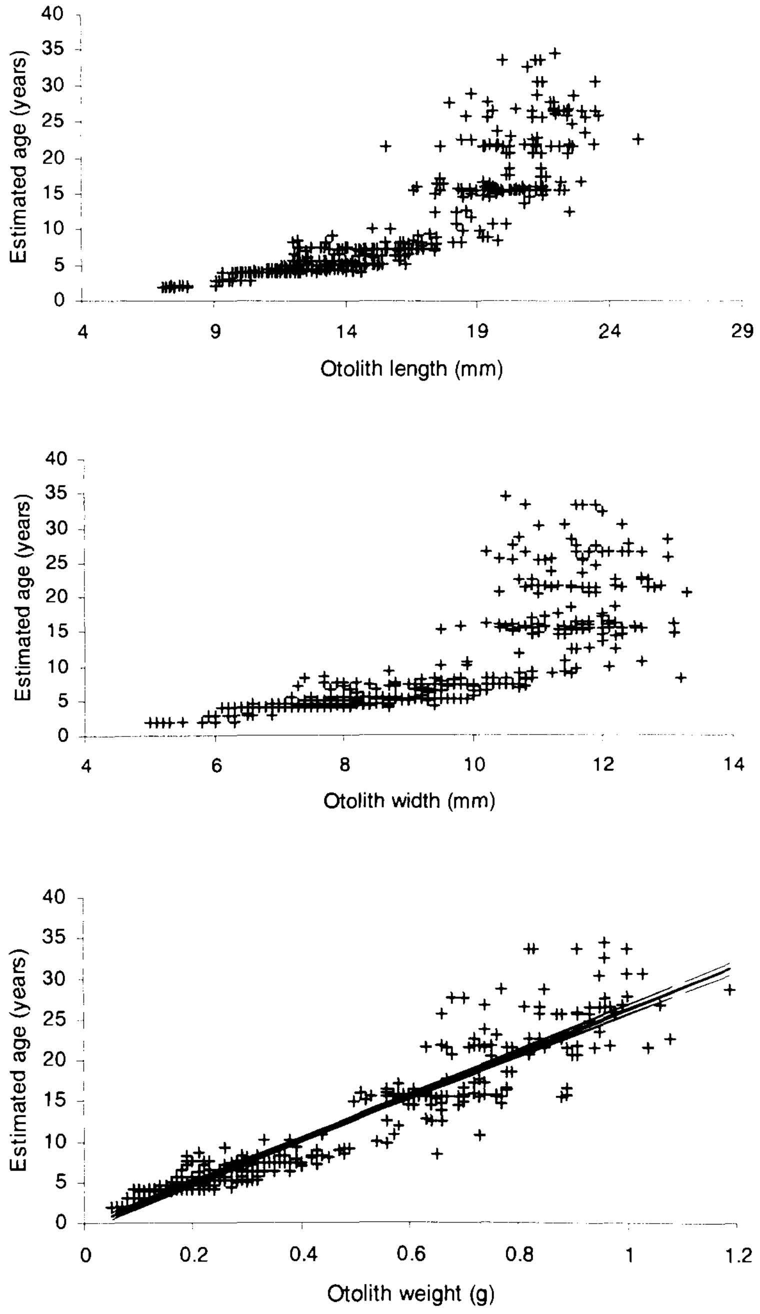


Fig. 3.10 Relationship between estimated age and otolith top) length, middle) width and bottom) weight for northern Spencer Gulf snapper. The solid line in the bottom figure indicates the predicted values from a linear regression and the dashed lines show the 95% CI of the regression.

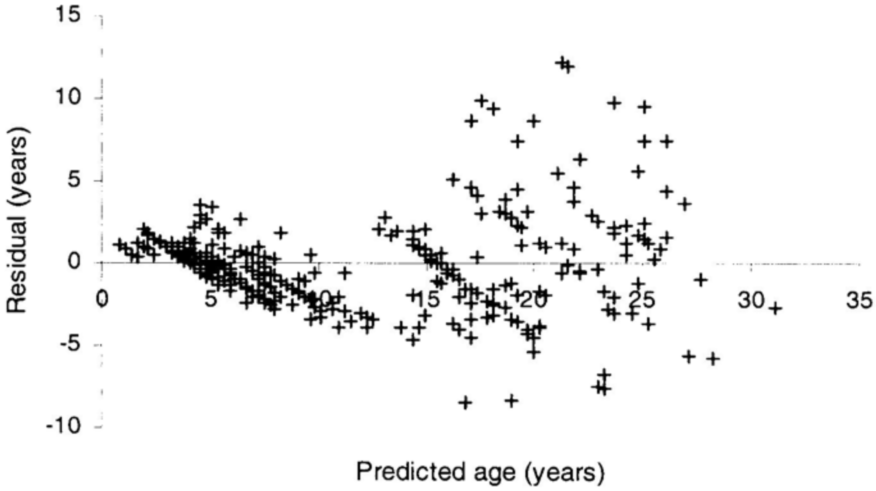


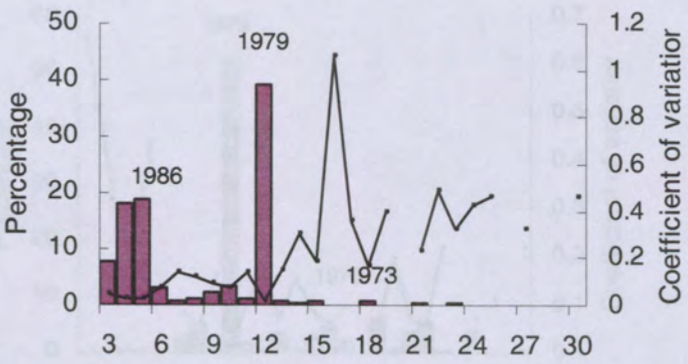
Fig. 3.11 Residuals of the age - otolith weight regression of Fig. 3.10c.

3.3.4 Age structures

Snapper ages of up to 34 years were recorded. Otoliths with counts of annuli up to 38 or 39 were present, but since agreement was not reached on the count, they were excluded from the final sample. Knowledge of the timing of annulus formation allowed an objective allocation of age to each fish. The algorithm from (Francis et al. 1992) was generally applicable, with fish < 5 years old forming a new annulus in November/December and older fish forming one from January to February. However, in contrast to (Francis et al. 1992), it was evident that fish older than 5 years can also show a new annulus in November and were observed with narrow (<20% previous increment) translucent margins in December.

The age structure of the handline caught snapper in 1991 showed the dominance of a strong 1979 yearclass (Fig. 3.12a). Very few fish were landed from cohorts spawned between 1980 and 1986 or before 1979. By 1994, the 1979 yearclass had virtually disappeared from the handline catch (Fig. 3.12b) and the catch was now dominated by recently recruited snapper from the 1990 and 1991 yearclasses and to a lesser degree 1988. The mean age of fish landed by this sector had decreased from 8.4 years in 1991 to 5.6 years in 1994.

a) 1991



b) 1994

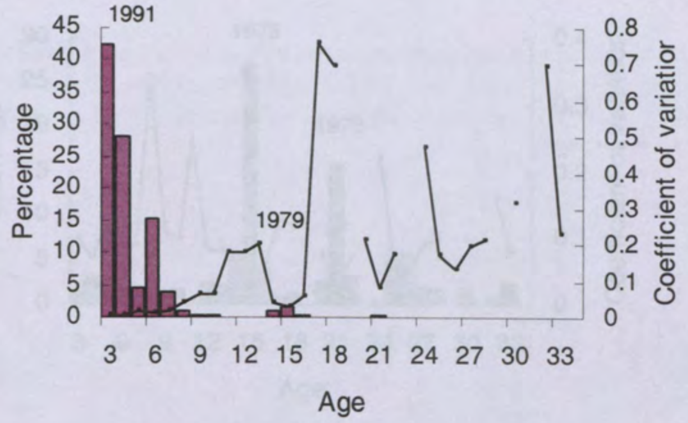


Fig. 3.12 Age structure of snapper caught by handline in northern Spencer Gulf in 1991 and 1994. The solid lines represent the coefficient of variation of each estimate of proportion at age. The years annotated on each graph refer to spawning years.

The age structure of the longline fishery in 1991 again showed the influence of the strong 1979 yearclass (Fig. 3.13a). In contrast to the handline catch, few fish from more recent yearclasses were evident and about 40% of the catch by number was from fish 15 – 25 years old. In 1994 the 1979 yearclass remained dominant (Fig. 3.13b) and with evidence also of a strong 1973 yearclass. It is also evident that no new strong yearclasses have recruited to the fishery, in contrast to the handline fishery.

a) 1991

b) 1994

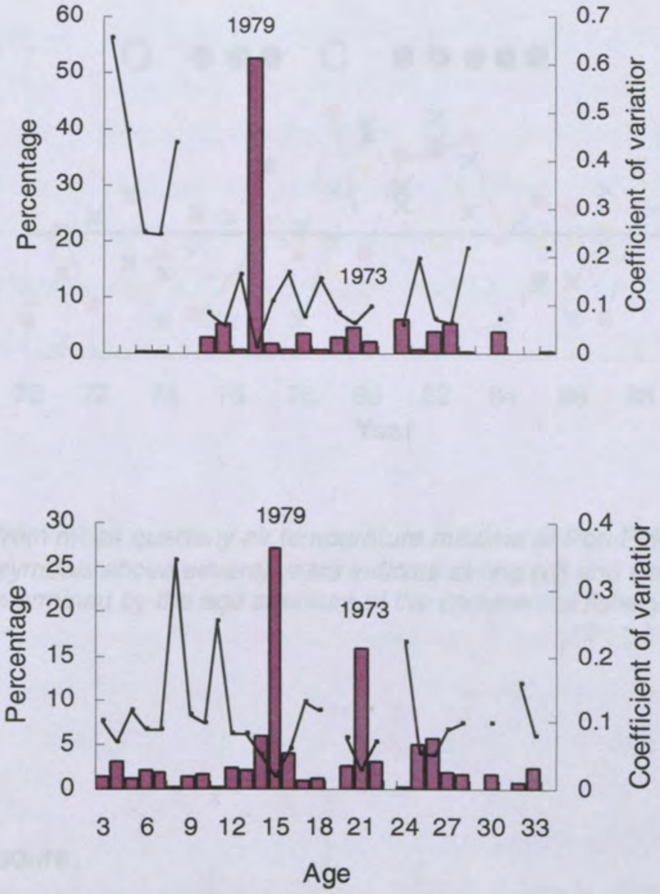


Fig. 3.13 Age structure of longline caught snapper in northern Spencer Gulf in 1991 and 1994. The solid lines represent the coefficient of variation of each estimate of proportion at age.

3.3.5 Yearclass strength and temperature

Summer (Jan-Mar) air temperature maxima were less than or equal to the 1970-1991 mean from 1970 to 1978 but were higher than the mean in nine out of the following 13 years (Fig 3.14). The highest summer value was recorded in 1979 and corresponds to a very strong yearclass, but the following three high values correspond to weak yearclasses. Autumn (Apr-Jun) maxima generally fluctuated by less than ± 1°C from the mean and there is little evidence that high or low extremes correspond to strong or weak yearclasses. High spring (Oct-Dec) temperatures (read from the year before yearclass strength symbols) precede both strong and weak yearclasses. In summary, a strong relationship linking high temperatures with strong yearclass strength and low temperatures with weak yearclasses is not apparent, with anomalies more common than supporting evidence.

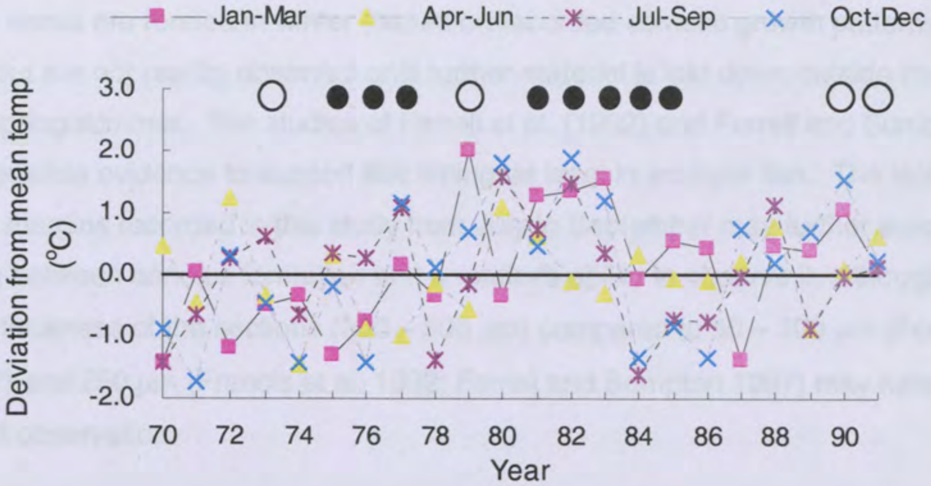


Fig. 3.14 Deviation from mean quarterly air temperature maxima at Port Pirie from 1970 to 1991. The symbols above several years indicate strong (O) and weak (•) year class strengths determined by the age structure of the commercial fishery catch.

3.4 Discussion

3.4.1 Ageing procedure

The results of the ageing component of this study showed that sectioned sagittal otoliths can be confidently used to age snapper from northern Spencer Gulf. Counts of annuli by different readers showed no systematic bias and were counted with high precision. Previous ageing studies of South Australian snapper have been based on scale readings and have recorded a maximum age of 23 years (Jones 1981; Jones 1984a). This study extends the maximum age by approximately 50% and supports the contention that scale ageing is unreliable for older fish (Paul 1976; Francis et al. 1992).

Annulus formation on sectioned otoliths has been recorded from July to February in other Australian and New Zealand populations (Francis et al. 1992; Ferrell et al. 1992; Ferrell and Sumpton 1997). Ferrell et al. (1992) took bi-monthly samples from 0^+ and 1^+ snapper maintained in captivity and recorded opaque margins from July to October, whereas wild caught 2^+ and 3^+ snapper from New South Wales and Queensland, Australia, showed few (or no) opaque margins from March to July and then increased to a maximum in November (Ferrell and Sumpton 1997). Francis et al. (1992) recorded annuli that were co-incident with the fluorescent marks made from oxytetracycline injections in November/December and February. They hypothesised that the annuli are formed in winter (based on recorded somatic growth patterns Paul (1976) but are not readily observed until further material is laid down outside the annuli in late spring/summer. The studies of Ferrell et al. (1992) and Ferrell and Sumpton (1997) provide evidence to support this timing, at least in younger fish. The lack of opaque margins recorded in this study from July to September may further support the time lag between annulus formation and a reader's ability to observe it, although the greater thickness of the sections (300 – 500 μm) compared to 50 – 100 μm (Ferrell et al. 1992) and 250 μm (Francis et al. 1992; Ferrell and Sumpton 1997) may have inhibited observation.

3.4.2 Otolith morphometrics

The laboratory processes of sectioning and interpreting snapper otoliths are time consuming. For routine annual stock assessment research projects, considerable savings could be made if a proxy for age could be determined from a simple measurement of size or weight of the otolith. Although the age – weight relationship showed more promise than length or width in this study (and radii and diameter in Francis (1992)), the scatter of residuals around predicted age provided no more precision than those measurements. Given the need for accuracy in age determinations in stock assessment, it is concluded that sectioning and interpretation of individual otoliths is required.

3.4.3 Length frequency distributions

The length frequency distributions generated from the market measuring program formed not only the basis for development of age length keys (Appendices 3.1 & 3.2) but also provided a further insight into the dynamics that occur in the catches of the fishery – between the two fishing methods operating in the fishery, seasonality and between years.

3.4.3.1 Fishing methods

While handlines and longlines both employ hooks for fish capture, the gear uses different size hooks, is most actively used at different times of the year and, to a degree, is set in different areas (see Chapter 2 for detailed descriptions of the fishery and its methods). Basically, fishers from each sector target a different subset of the snapper population. The handline catch spanned most of the size range of northern Spencer Gulf snapper but the longline catch was limited to the largest fish (with a very small percentage of smaller fish). It is interesting to note that the most recent year of market measuring (2002) recorded a more even spread of size classes in the longline fishery (Fowler et al. 2003) than is recorded in this study. This may be due to the influx of another strong yearclass from 1997 but is also possibly due to an expansion of the target range for the fishery, which has endured very low catches since 1998 (Fowler et al. 2003).

3.4.3.2 Seasonal changes

The seasonal length frequency distributions evident in the handline catch of 1991 suggests a pattern of dispersal and aggregation, probably related to spawning activity, may be occurring within the fishing grounds. The larger fish move onto the fishing grounds in spring which coincides with the time that spawning takes place (Crossland 1977b; Jones 1981; Scott and Pankhurst 1992; Chapter 5). The larger fish remain on the fishing grounds during summer but disperse in autumn. Smaller fish (i.e. LML – 40 cm LCF) are present in the catch throughout the year and may not participate in the dispersal / aggregation behaviour to the same extent as the larger fish. The seasonal pattern was not as evident in 1994 but the larger fish were generally absent from the handline catch during that period. Similar patterns have been recorded from measuring programs in 2000, 2001 and 2002 (Fowler et al. 2003). This dispersal / aggregation behaviour is further discussed in Section 3.4.4 and Chapter 6.

In contrast to the handline catch, the size frequency distribution of the longline catch showed little seasonal or inter-annual differences (comparison of data from Jones (1984a) and this study).

3.4.3.3 Inter-annual changes

The commercial snapper catch in northern Spencer Gulf had been the subject of a series of market measuring programs between 1978 and this study and the length frequency distributions of the handline catches showed some significant changes during that period (Fig. 3.15).

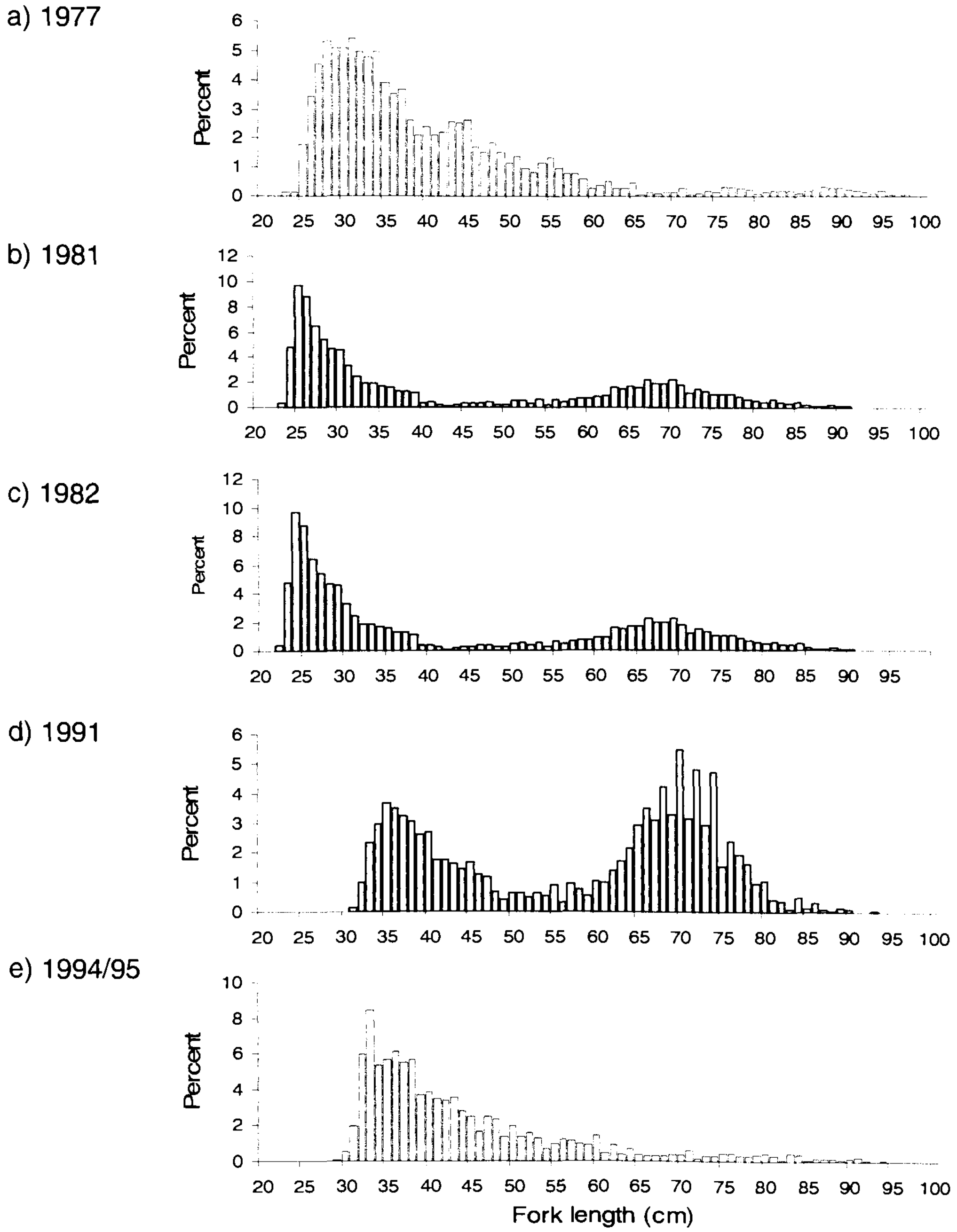


Fig. 3.15 Length frequency distributions of handline catches in northern Spencer Gulf between 1978 and 1995/96. All distributions have been plotted on the same x-axis scale for comparative purposes.

The distributions can best be compared by reference to the relative magnitude of the mode representing the larger fish (say 60 – 80 cm LCF). The mode is virtually absent in 1977, appears in 1981 and 1982, is dominant in 1991 and again is absent in 1994/95. Handline fishing practices differed little over this time – global positioning satellite navigation was introduced but the fishing gear remained similar. The changing distributions have continued from 2000 to 2002 (Fowler et al. 2003). An explanation is given for this pattern by the catch at age in Section 3.4.4.

The lengths of snapper taken by recreational fishers were also measured during a twelve month survey in northern Spencer Gulf in 1995/96 (McGlennon and Kinloch 1997). The recreational catch in 1995/96 showed strong similarities to the commercial catch of 1994/95 (Fig. 3.16). The recreational fishers use similar gear to the commercial handline fishers and, in general, fish in similar locations. It can be reasonably concluded that they are fishing the same population.

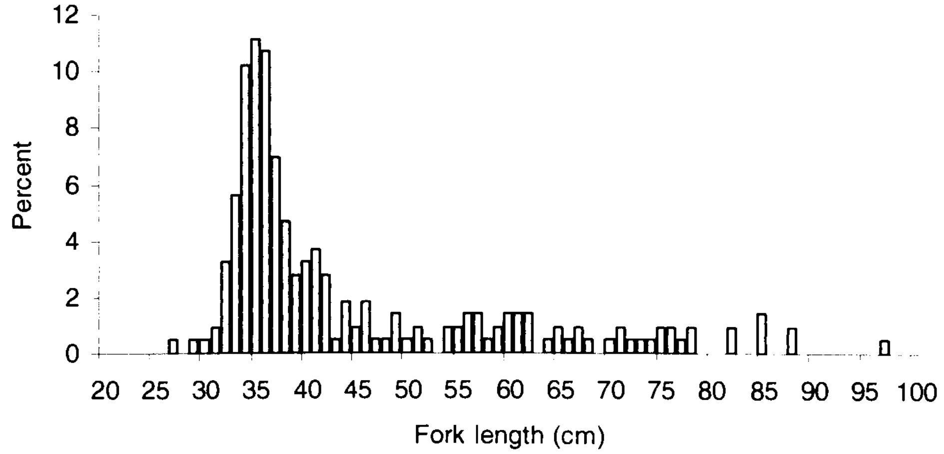


Fig. 3.16 Length frequency distribution of the recreational snapper catch in northern Spencer Gulf 1995/96 (from McGlennon and Kinloch 1997).

3.4.4 Catch at age

The strong differences in length structure of the handline and longline catches were similarly depicted in the age structures, and there was very little overlap in catch at age between the two sectors. Snapper from the 1991 yearclass recruited to the handline fishery in late 1994 and were numerically dominant in the catch. Very few fish greater than seven years old were recorded, contrasting with the age structure of the 1991 handline catch which was dominated by twelve year old fish from the 1979 yearclass. The stark contrast between the two sampling years is interpreted as 1) the results of highly variable yearclass strength and 2) the presence of few strong yearclasses in the spawning aggregations which support this handline fishery. The handline fishery primarily targets pre-spawning and spawning aggregations during late spring and summer. During 1991, the handline catch was dominated by the strong 1979 yearclass (12+ fish) but, by 1994, this yearclass was almost non-existent in the catch.

In contrast, the longline catch was dominated by the 1979 yearclass in both samples. As the longline fishing grounds lie within the same area as the handline fishery, it appears that the older ($>15^{+}$) fish may no longer participate in spawning aggregations. Conversely, the relative lack of smaller (younger) fish in the longline catch operating from autumn to spring, suggests that the fish contributing to spawning aggregations disperse away from northern Spencer Gulf during those months.

3.4.5 Relative yearclass strength

The catch at age results of this study clearly demonstrate that highly variable yearclass strength occurs in South Australian snapper. Strong yearclasses were evident from 1973, 1979, 1990 and 1991 whereas the yearclasses from 1974 to 1978, and from 1980 to 1986 (or 1988) were relatively weak. The relative strength of the newly recruited 1991 yearclass was interpreted cautiously at the time of the study as it had not been subjected to prolonged fishing mortality. However, more recent age compositions have shown the 1991 yearclass to be very strong (Fowler et al. 2003). It appears that the pattern of infrequent strong yearclasses interspersed with relatively poor yearclasses has continued – age compositions from the fishery to 2002 show that 1992 to 1996 inclusive, and 1998 and 1999 were poor yearclasses, and recruitment trawl surveys have provided no indication of better yearclasses to 2002 (Fowler et al. 2003). Variable yearclass strength has previously been demonstrated for this species in Victoria, New Zealand and Japan (Matsumiya et al. 1980; Kojima 1981; Francis 1993; Davies and Walsh 1995; Walsh et al. 1995; Coutin 1997). Comparisons of the strong yearclasses reported in the New Zealand and Australian studies show few similarities (Walsh et al. 1995) and it appears that the processes influencing yearclass strength operate at relatively small (i.e. less than regional) spatial scales.

The relationship between temperature and yearclass strength has been investigated for the Hauraki Gulf snapper population after Paul (1976) provided qualitative evidence of a relationship between air temperature (as a proxy for water temperature) in the spawning months of November and December. The relationship was empirically tested using annual yearclass strength (based on the abundance of 1^+ fish) and water temperature, and a strong positive correlation was recorded for temperature in both summer (Jan – Mar) and autumn (Apr – Jun) (Francis 1993).

In this study, an initial examination of data similar to those used by Paul (1976) provided little clear evidence that such a relationship might hold in Spencer Gulf. For example, the summer temperature was highest in 1979 when a very strong yearclass was spawned but the next three highest temperatures occurred from 1981-3 when weak yearclasses occurred. The lowest summer temperatures occurred in 1970, 1972, 1975 and 1987 that correspond to weak yearclasses. High autumn temperatures corresponded to both strong and average yearclasses. However, the autumn temperature would have predicted a weak 1979 yearclass. A qualitative analysis such as this is clearly limited and the establishment of a regular juvenile abundance survey (Fowler 2002) will provide the opportunity to empirically test the relationship in coming years.

Long-lived species such as snapper are not normally prone to recruitment induced fluctuations in biomass unless, for example, a series of strong or weak yearclasses occur. In the South Australian fishery, it is apparent that a series of weak yearclasses occurred through the mid 1970s and also from the early to mid 1980s, and the high variability in recruitment strength could explain the fluctuations in commercial snapper catches over the last 20 years. The catch of the handline fishery strongly influences total catch and it in turn appears to have been dependent on very few strong yearclasses over the last 20 years to 1994. More recent work demonstrates that this pattern will continue into the future.

Recruitment variability is common in marine species and results in two fundamental sources of uncertainty in stock assessments and management of the fishery (Sissenwine et al. 1988). The variability obscures the functional relationship of the stock-recruitment relationship which in turn results in uncertainty in setting biological reference points and yields. Secondly, it requires a probabilistic approach to providing management advice and in decision making. The latter is addressed in the population model developed in Chapter 8 by use of Monte Carlo simulations.

Appendix 3.1 1991 age length key (proportion at age) for northern Spencer Gulf snapper from otolith ageing of 385 fish.

Yearclass	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	1979	1978	1977	1976	1975	1974	1973	1972	1971	1970	1969	1968	1967	1966	1965	
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	21	22	23	24	25	27	30	
FL cm																											N
16	1.00																										3
17	0.67	0.33																									1
18	1.00																										3
19	1.00																										7
20	0.86		0.14																								4
21	1.00																										3
22	0.67	0.33																									7
23	0.57	0.14	0.29																								7
25	0.14	0.14	0.57	0.14																							3
26		0.67	0.33																								6
27	0.17	0.33	0.33	0.17																							7
28		0.14	0.86																								9
29	0.22		0.78																								6
30		0.17	0.67	0.17																							13
31			0.92		0.08																						14
32		0.07	0.50	0.43																							28
33			0.32	0.57	0.11																						18
34			0.33	0.44	0.22																						14
35			0.36	0.64																							14
36			0.21	0.57	0.21																						15
37			0.13	0.80	0.07																						9
38			0.11	0.67	0.22																						8
39			0.25	0.50	0.25																						5
40			0.20	0.40	0.40																						3
41				0.33	0.67																						1
42					1.00																						4
43				0.50	0.50																						2
44					1.00																						1
47					1.00																						2
48					1.00																						1
51					1.00																						1
52					1.00																						3
53					0.67	0.33																					2

Yearclass	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	1979	1978	1977	1976	1975	1974	1973	1972	1971	1970	1969	1968	1967	1966	1965	
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	21	22	23	24	25	27	30	
FL cm																											N
55						0.50	0.50																				1
59						1.00																					1
60								1.00																			2
61									0.50	0.50																	5
62						0.20	0.20					0.60															3
63						0.33			0.33			0.33															3
64												1.00															6
65											0.17	0.83															4
66												1.00															3
67										0.33		0.67															4
68												1.00															5
69												1.00															1
70												1.00															8
71									0.25	0.25		0.50															9
72										0.11		0.67	0.22														7
73											0.14	0.86															3
74												1.00															7
75									0.14	0.14		0.71															8
76												0.75	0.13		0.13												7
77									0.14	0.29		0.57															15
78										0.13		0.67		0.07				0.13									6
79												1.00															6
80												0.83								0.17							8
81									0.13	0.25		0.38						0.25									4
82												0.50			0.25			0.25									4
83												0.25					0.25	0.25	0.25								5
84												0.20		0.20	0.20									0.20		0.20	7
85												0.71				0.14		0.14									2
86															0.50							0.50					4
87												0.25										0.50	0.25				2
88																				0.50			0.50				1
90																									1.00		1
91																	1.00										3
92												0.33								0.33			0.33				2
93																			0.50	0.50							1
N	29	11	75	77	32	5	2	1	7	12	2	97	3	2	4	1	2	7	2	4	1	3	3	1	1	1	385

Appendix 3.2 1994 age length key (proportion at age) for northern Spencer Gulf snapper from otolith ageing of 468 fish.

Yearclass	1994	1993	1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	1979	1978	1977	1976	1975
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
FL cm																				
17	0.17	0.83																		
18		1.00																		
19		1.00																		
20		1.00																		
21		1.00																		
23			0.80	0.20																
24			0.67	0.33																
25			0.29	0.71																
26			0.25	0.75																
27				1.00																
28				1.00																
30				1.00																
31				1.00																
32				1.00																
33				0.86	0.14															
34				0.82	0.09			0.09												
35				0.83	0.17															
36				0.80	0.07	0.07	0.07													
37				0.30	0.40		0.30													
38				0.50	0.25		0.25													
39				0.54	0.31		0.08	0.08												
40				0.45	0.45			0.09												
41				0.17	0.50	0.17	0.17													
42				0.25	0.50	0.13	0.13													
43				0.30	0.40	0.10	0.20													
44					0.86			0.14												
45				0.14	0.57		0.29													
46				0.33		0.33	0.33													
47				0.33	0.50		0.17													
48				0.20	0.80															
49					0.60	0.20	0.20													
50					0.50	0.10	0.40													
51					0.44	0.11	0.44													
52					0.60		0.20		0.20											

Yearclass	1994	1993	1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	1979	1978	1977	1976	1975
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
FL cm																				
53					0.50	0.17	0.33													
54					0.50	0.25	0.25													
55						0.40		0.60												
56					0.13	0.13	0.75													
57					0.29		0.43	0.14		0.14										
58						0.40	0.20	0.20	0.20											
59							1.00													
60						0.17	0.67				0.17									
61					0.17		0.33	0.33	0.17											
62						0.20	0.40	0.20	0.20											
63							0.33								0.33	0.33				
64							1.00													
65								1.00												
66								1.00												
67							0.50	0.50												
68							0.40	0.20	0.20	0.20										
69							1.00													
70															1.00					
71								0.50	0.50											
73								1.00												
74																1.00				
75																	1.00			
76										0.50					0.50					
77															0.50	0.50				
78															0.33	0.67				
79								0.25			0.25					0.50				
80											0.25				0.25	0.25				
81												0.20			0.20	0.60				
82														0.14	0.14	0.71				
83														0.08	0.08	0.58				
84													0.15			0.46				
85										0.10				0.10		0.40				
86													0.07		0.07	0.43	0.07			0.07
87																0.08		0.08	0.08	
88													0.15		0.08		0.08	0.08		
89																			0.09	
90																0.07	0.21			

Yearclass	1994	1993	1992	1991	1990	1989	1988	1987	1986	1985	1984	1983	1982	1981	1980	1979	1978	1977	1976	1975
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
FL cm																				
91																0.17				
92																				
93																0.20				0.20
94																				
95																				
97																				
N	1	12	9	122	73	17	53	20	6	4	3	1	5	3	11	44	6	2	2	2

Appendix 3.2 (cont)

Yearclass	1974	1973	1972	1971	1970	1969	1968	1967	1966	1965	1964	1963	1962	1961	1960	
Age	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
17																6
18																2
19																2
20																1
21																2
23																5
24																3
25																7
26																4
27																6
28																7
30																2
31																9
32																11
33																21
34																11
35																12
36																15
37																10
38																4
39																13
40																11
41																6
42																8
43																10
44																7
45																7
46																3
47																6
48																5
49																5
50																10
51																9

Yearclass Age	1974 21	1973 22	1972 23	1971 24	1970 25	1969 26	1968 27	1967 28	1966 29	1965 30	1964 31	1963 32	1962 33	1961 34	1960 35	
52																5
53																6
54																4
55																5
56																8
57																7
58																5
59																1
60																6
61																6
62																5
63																3
64																2
65																1
66																2
67																2
68																5
69																1
70																1
71																2
73																1
74																1
75																1
76																2
77																2
78																3
79																4
80		0.25														4
81																5
82																7
83		0.17	0.08													12
84	0.08					0.08	0.08	0.08	0.08							13
85		0.10				0.10					0.10			0.10		10
86	0.07	0.07				0.07					0.07					14
87	0.08	0.15		0.08		0.15	0.23								0.08	13
88	0.08	0.15	0.08			0.08	0.23									13
89		0.36	0.09			0.09		0.09	0.09				0.09	0.09		11

Yearclass	1974	1973	1972	1971	1970	1969	1968	1967	1966	1965	1964	1963	1962	1961	1960	
Age	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
90	0.07	0.21	0.07			0.07		0.07	0.07					0.14		14
91		0.17	0.08		0.08	0.08	0.25	0.08			0.08					12
92		1.00														1
93			0.20			0.20	0.20									5
94							1.00									1
95		1.00														1
97				1.00												1
N	5	20	6	2	1	10	12	4	3		3		1	4	1	468

Chapter 4. The effect of temperature and salinity on the development rate, hatching rate, larval length and larval viability of *Pagrus auratus.*

4.1 Introduction

The distribution of *Pagrus auratus* in the southern hemisphere extends from New Zealand in the east to Western Australia in the west, and from latitudes 21°S to >45°S (MacDonald 1982). Water temperatures throughout this distribution range from <12^{0}C in southern New Zealand to >26^{0}C on the North-West Shelf, Western Australia. Salinities range from around 35‰ for the oceanic waters of the continental shelf to 60 - 70‰ for the hypersaline waters of Shark Bay (references in Johnson et al. 1986; Edmonds et al. 1999). Clearly the species has a broad physiological tolerance for a wide range of water temperatures and salinities. For northern Spencer Gulf (NSG), water temperatures range from 12^{0}C in winter to 25^{0}C in summer, with salinities from 36 to 48‰ (Bye and Whitehead 1975; Nunes and Lennon 1986).

Temperature and salinity have significant effects on the development of fish eggs (Alderdice 1988; Blaxter 1988). Temperature plays a critical role in the rate of development while, at extreme levels, both temperature and salinity affect normal development and survival. The development of eggs of marine fishes is known to be less tolerant of changes in temperature and salinity than are anadromous and freshwater species, particularly in the early development stages (Tytler and Ireland 1993).

The effects of variation in water temperature and salinity on the development of eggs of *P. auratus* are of particular interest to this study. The use of the Daily Egg Production Method (DEPM) to calculate biomass (Chapter 5) depends on assigning an age to each egg sampled during plankton sampling. To enable this, it is necessary to establish a relationship between the developmental stage of the egg and the temperature and salinity at which the egg has developed, i.e. the effect of temperature and salinity on the rate of development of the eggs.

Some information is available on the development of sparid eggs at different temperatures and salinities. Apostolopoulos (1976) studied hatching rate, hatching time and total body length of *Pagrus major* in Japan at temperatures from 8 – 33^{0}C and salinities from 11.03 – 34.80‰. A more comprehensive study for this species investigated incubation period, hatching rate and morphogenesis at temperatures from 12.7 – 29.7^{0}C and salinities from 6 – 54‰ (Mihelakakis and Yoshimatsu 1998). A similar study investigated the same features of the eggs of *Sparus sarba* at temperatures from 13 – 23.5^{0}C and salinities from 8 – 52‰ (Mihelakakis and Kitajima 1994). Freddi et al. (1981) investigated the responses of *Sparus auratus* eggs and larvae to temperatures of 18 – 26^{0}C and salinities from 5 – 70‰. Finally, Cassie (1956) and Crossland (1980) both described the development of eggs of *P. auratus* in New Zealand at 21^{0}C.

Water temperatures in NSG during the plankton sampling (see Sect 5.3.1 for sample data from plankton cruises during this period) ranged from 17.3 - 23.9^{0}C and salinities ranged from 36.4 – 42.7‰. The study of *P. major* by Mihelakakis and Yoshimatsu (1998) covered this temperature and salinity range but was not published at the time of this experiment (27/8/97). However, the taxonomic uncertainty that exists between northern and southern hemisphere populations (Perez-Enriquez and Taniguchi 1999; Tabata and Taniguchi 2000) provided justification for further investigation of *P. auratus*. Furthermore, that study provides incubation periods rather than a full description of egg development. The primary aim of the study described in this chapter was to investigate environmental effects on the rate of development of *P. auratus* eggs **during** development, rather than providing hatching times.

From an ecological perspective, the effects of temperature and salinity on measures of spawning success are of particular interest to an understanding of the biology of this species. The strength of the yearclass from a particular spawning may be determined by environmental effects on incubation period, hatching rate and larval size and viability. The aims of this experiment were therefore:

- primarily, to establish a relationship between the development of eggs of *P. auratus* and the independent variables of temperature and salinity;
- and secondarily, to investigate the effects of salinity and temperature on a) incubation period, b) hatching rate, c) larval length and d) larval viability.

4.2 Methods

This experiment required a supply of fertilized eggs at the earliest development stage possible. Attempts were made to collect fertilized eggs from snapper broodstock which had been maintained at the marine laboratories of the South Australian Research and Development Institute (SARDI) for aquaculture purposes for a number of years. The fish were maintained in 30,000 l outdoor tanks with flow-through water supply from the adjacent Gulf St Vincent (source 500 m from the coastline). The water temperature was not controlled in these outdoor tanks and therefore reflected the source seawater (approximate range from 12^{0}C to 22^{0}C through the year). The broodstock were transferred indoors when spawning was to be induced. They were placed in 10,000 l tanks in which the photoperiod and water temperature could be controlled to simulate the lengthening days and rising water temperature indicative of the natural spawning season in late spring and summer (Jones 1981). The ovaries of the female broodstock were sampled regularly by catheter to assess ovarian condition in the lead up to spawning. Final oocyte maturation was induced by injection of an analogue of lutenising hormone releasing hormone when vitellogenesis was completed (oocyte diameter > 400 μm) (W. Hutchison, SARDI, pers. com.).

Two different methods of obtaining fertilized eggs were tried after the commencement of spawning activity was determined by the presence of eggs in the tank overflow filter. The first involved removing individual fish from the tank, anaesthetising them in a plastic bin containing a benzocaine solution, and then manually stripping ovulated eggs from the oviduct. This was done by inverting the fish, applying manual pressure to the abdomen and collecting the ovulated eggs in a plastic dish. A similar method was used to obtain sperm. The sperm were mixed with the eggs and seawater was added to promote fertilization. In the second method, the fish (males and females together) were left in the tanks to spawn naturally and the fertilized eggs were captured through the fine mesh filter placed on the tank outflow. Since snapper spawn daily over an extended period (Scott et al. 1993), these methods could be tried repeatedly. A number of unsuccessful attempts were made at obtaining eggs using both of these methods. Eggs captured in the tank outflow showed low fertilization and development rates suggesting a problem with the viability of the eggs. This has previously been observed with snapper held in captivity for extended periods such as these had (Foscarini 1988).

Ultimately, the fertilized eggs were obtained from an external source – the Spencer Gulf Hatchery located at Port Augusta in South Australia. The eggs were collected from the tank water outflow after natural fertilization in the tanks. They were transported to the SARDI laboratory in a 20 litre container of oxygenated seawater which, on arrival, was at 20.7^{0}C and 37.9‰.

4.2.1 Experimental procedure

The experiment aimed to quantify the development rate of snapper eggs at a range of temperatures (T) of 18, 21 and 24^{0}C, and at a range of salinities (S) of 36, 40, 44 and 48‰. The experiment was set up according to a factorial design with three replicates at each of the T/S combinations. The 36 experimental containers were clear plastic bottles which were placed in 3 plastic bins (one for each T) which acted as water baths (Fig. 4.1).

Fig. 4.1 The plastic experimental containers were maintained in temperature controlled water baths at three experimental temperatures.

The SARDI laboratory was equipped with a computer based water management system. Water outlets terminated in mixing chambers which received both heated and chilled seawater. The temperature of water produced by each outlet was then set and monitored via a computer interface, with a temperature sensor fixed in each water bath to provide feedback to the computer. The temperature of each bath was set initially to 20.7°C to match the temperature of the transport water. Three replicate containers of each of the four salinities were placed randomly throughout each bath. The containers were filled with 800ml of seawater obtained from the laboratory's flow through system. Elevated salinities (> 36‰) were obtained by adding "Instant Ocean" salt mix.

The eggs were firstly transferred from the transport container into a smaller container, and were then added to the experimental containers by drawing approximately 30 ml of water in a pipette and adding it to each container. The 30 ml of water contained between 247 and 353 eggs (counted at the conclusion of the experiment), giving about 10,800 eggs in the experiment. The water flowing into the water baths was then changed incrementally to the experimental temperatures at a rate of approximately 3°C per hour. To check on the development of the eggs at this time (1815 hours), a reference sample was taken after the transfers and fixed in 10% formalin seawater solution.

Egg samples were drawn from each of the three replicates from each T / S combination at irregular times for the following 38 hours (Table 4.1). Approximately 10 ml of water was drawn by pipette and the contents put into jars containing 10% formalin sea water solution. This volume contained between 4 and 37 eggs (mean = 15.3). Samples continued to be drawn until 50% of the remaining viable (floating) eggs had hatched. The experiment was concluded at each of the experimental temperatures at 120 temperature hours (T°C * time (hours)) after 50% hatching was observed. The remaining contents of each sample were fixed in formalin and the water in each container was tested for final salinity readings.

Table 4.1 Elapsed time (hours) for egg sampling at each temperature.
The eggs were transferred to the experimental containers at 1800 hours (time = 0).

Sample \ T°C	18°	21°	24°
1	1.9	1.9	1.9
2	8.6	5.6	5.1
3	15.0	9.0	8.75
4	19.6	11.9	11.6
5	24.25	15.2	14.3
6	31.5	18.2	17.6
7	40.0	21.25	

4.2.2 Egg staging and ageing

The developmental stages of *P. auratus* eggs have been described by Cassie (1956) and Crossland (1980). Crossland's study was undertaken at 21°C and his descriptions were based on stages which occured at approximately equal time intervals. His Figure 10 was used as the basis for discriminating between stages (Table 4.2).

Table 4.2 Descriptions of *P. auratus* egg stages used in DEPM survey.

Stage	Description
1	up to 16 cells
2	> 16 cells but individual cells visible
3	individual cells indistinguishable but prior to epiboly
4	blastodisc starting to enlarge at periphery of blastodisc
5	blastodisc about 1/3 of yolk and germ ring starting to thicken
6	blastodisc about ½ yolk and germ ring distinct
7	blastodisc covers ¾ yolk and gastrulation commenced – embryo visible
8	embryo 2/5 yolk with rudimentary head; blastopore small adjacent to caudal region
9	blastopore closed, optic vesicles visible, tail formed
10	tail flat, embryo < 50% yolk, first myotomes visible centrally
11	embryo ½ yolk, optic vesicles clear
12	embryo > 50% yolk, tail thickened at base
13	tail lifted from yolk at base, embryo straight
14	tail with some curvature
15	embryo > 75% yolk, finfold evident around tail, oil droplet still central
16	Long tail, oil droplet ventral in yolk sac

The egg development experiment provided an accurate estimate of the elapsed time between stages after the eggs were obtained. However, the difficulties of obtaining newly fertilised eggs meant that the eggs used had an unknown time of fertilisation, and an estimate of this time was fundamental for quantifying the entire developmental model. Two approaches were used: one for the eggs obtained and maintained at ≈21°C and a second for those maintained at 18°C and at 24°C.

The developmental rate of Crossland (1980) was used for the 21°C estimate. The temperature of the transport water was 20.7°C on arrival at SARDI and it was assumed that this had been similar during transport. A reference sample had been taken at 1815 hours in the laboratory and those eggs were staged. The reference sample showed eggs at three different developmental stages – 2, 4 and 5 (Table 4.2). The (weighted) average age ($\bar{a}_r$) of this sample was calculated by

$$\bar{a}_r = \frac{\sum_{j=1}^{j} n_j a_j}{\sum_{j=1}^{j} n_j} \qquad (4.1)$$

where n_j is the number of eggs of the *j*th stage and a_j is the age of the *j*th stage egg according to its rate of development in Crossland (1980) (Miranda et al. 1990). The average age of the sample was calculated as 7.27 hours, with most eggs being stage 4. The mean time of fertilisation was then estimated by subtracting the average age (7.27 hours) from the time the reference sample was taken (1815 hours) to give a time of 1100 hours (rounded). The age of stages 1, 2, 3 at this temperature was estimated by dividing the elapsed time in equal 2 hour periods, again following the equal time divisions of (Crossland 1980).

This calculation provided a means of estimating ages of egg stages at 21°C but another method was required for 18°C and 24°C. Mihelakakis and Yoshimatsu (1998) investigated the incubation period (*I*) of the closely related red sea bream *Pagrus major* and found a curvilinear relationship with temperature (T°C) of

$$I = 27{,}598.9003T^{2.2348} \qquad (4.2)$$

This relationship predicted a time to hatch of 43.2 hours for 18°C and 22.7 hours for 24°C. The elapsed time between the eggs being placed in the experimental containers and the observed time at 50% hatch (mean = 32.7 hours at 18°C and 18.1 hours at 24°C) was subtracted from these estimates – the remainder provided an estimate of the time to develop to stage 4 at 18°C and 24°C. Again, this time was sub-divided equally for the three stages 1, 2 and 3. The (pseudo) time of fertilisation for these temperatures was 0800 for 18°C and 1350 hours for 24°C.

4.2.3 Analysis

The effect of temperature and salinity was analysed separately for egg development rates, incubation period, hatching proportion, and larval length and viability.

4.2.3.1 Relationship between temperature and egg development rates

The effect of salinity was shown not to have a significant effect on the incubation period (Sect. 4.3.2) and so the developmental model was based only on temperature as an independent variable. Lo (1985) described the relationship between the age of northern anchovy (*Engraulis mordax*) eggs and the stage of their development as

$$y_{i,t} = a\, e^{(bt+ci)}\, i^{d} \qquad (4.3)$$

where $y_{i,t}$ is the average age of the ith stage egg at temperature t°C and b, c and d are coefficients common to all stages and temperatures. To fit a similar model for snapper eggs, therefore, ages of the eggs at different stages were needed at the three experimental temperatures. These were obtained by:

1) assigning a stage to each egg based on the classifications in Table 4.2
2) assigning an age to each egg (calculated as the sampling time minus the estimated spawning time for that T)
3) calculating an average age for each stage was calculated using Eq. 4.1 (as single stage eggs were often recorded from different time samples, and therefore assigned different ages)
4) fitting the model of Eq. 4.3 to the average age for each stage at each T.

The model was fitted using non-linear least squares methods in JMP and SAS software and the data were weighted by the number of eggs recorded in each stage.

4.2.3.2 Effect of temperature and salinity on incubation period

As the experimental T/S conditions were only applied after eggs had begun development, their effect on incubation period (defined as time to 50% hatch; Pauly and Pullin (1988) was analysed from the time the eggs were placed in the containers. Experimental salinities were already established in the containers and water temperatures were stabilised at experimental temperatures within one hour. The data used were the elapsed time to 50% hatch (hours) and were analysed by two factor analysis of variance (ANOVA) with temperature and salinity as fixed factors. This and subsequent analyses used a significance level of 0.05 and the residuals were plotted against predicted values to assess homogeneity of variance.

4.2.3.3 Effect of temperature and salinity on hatching proportion

As each sample was drawn from the containers, the non-viable eggs were counted in addition to counting and staging the viable eggs. Eggs were classified as non-viable if they showed no development, had ruptured internal cells and / or were opaque. Hatching success was defined as the sum of viable eggs during sampling plus viable and non-viable larvae at the conclusion of sampling, and was expressed as a proportion of all eggs and larvae in each container. The effect of T and S on hatching success was tested by two factor ANOVA, with the proportions p first transformed by

$$p' = \arcsin \sqrt{p} \qquad \text{(Zar 1984) (4.4)}$$

4.2.3.4 Effect of temperature and salinity on larval length

At the conclusion of the experiment (120 temperature hours after 50% hatch), all remaining eggs and larvae were preserved for later analysis. Ten larvae were randomly selected from each container from each T/S combination (n = 360), and their total length TL (μm) measured using the image analysis software Video Pro 32. Three factor ANOVA (temperature, salinity and container as factors) was initially used to analyse the length measurements. However, the containers were not significantly different from each other (P = 0.953) and the analysis was subsequently simplified to a two factor ANOVA.

4.2.3.5 Effect of temperature and salinity on larval viability

Larval viability was defined as the proportion of larvae which exhibited normal development. Larvae were classified as viable or non-viable on the basis of the curvature of the body, with viable larvae exhibiting straight or near straight notochords while non-viable larvae had moderate to severe body curvature (Lee and Menu 1981; Freddi et al. 1981; Walsh et al. 1991). The data were transformed according to by Eq. 4.4 and analysed with a two-way ANOVA.

4.3 Results

4.3.1 Relationship between temperature and egg development

Salinity was shown not to have a significant effect on incubation period (Sect. 4.3.2) and so the only independent variable considered in the developmental model was temperature. The initial analysis was made using the 4 parameter model of Lo (1985) (Eq. 4.3) but the parameter *c* approached zero and contributed little to the fit of the model. The model was therefore re-estimated without *c* and resulted in a best fit ($r^2 = 0.99$) when

$$y_{i,t} = 36.158 \,.\, e^{(-0.12t)} \; i^{0.827} \tag{4.5}$$

with standard errors for a, b and d of 0.516, 0.001 and 0.003 respectively. The development rate decreased with increasing temperature (Fig. 4.2).

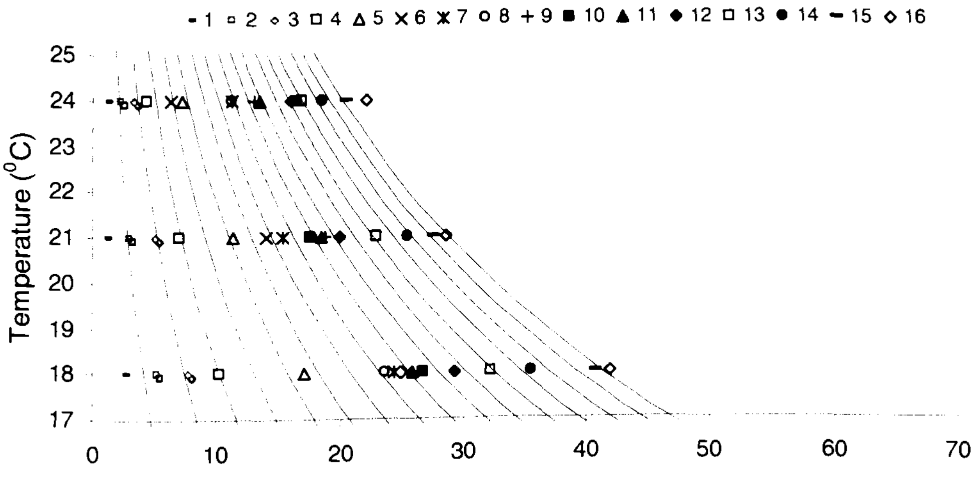


Fig. 4.2 Rate of development of P.auratus eggs at different temperatures.
The 16 stages are described in Table 4.2. The solid lines represent the development rate for each stage described by Eq. 4.5.

4.3.2 Effect of temperature and salinity on incubation period

Incubation period reduced considerably with increased temperature but was not significantly affected by salinity. The elapsed time from placing the eggs in their experimental treatments until 50% hatch varied from a minimum of 17.25 at 24°C to a maximum of 33.75 hours at 18°C (Table 4.3). The two factor ANOVA showed a significant difference between temperatures but not between salinities or the T * S interaction (Table 4.4). Although the effect of salinity was not statistically significant, there was a consistent small increase in incubation period of 1 – 1.5 h within each temperature from 36 - 48‰ (Table 4.3).

Table 4.3 Elapsed time to 50% hatch after eggs were placed in the experimental treatments.

Temperature (°C)	Salinity (‰)	Time to hatch (hours) Replicate 1	2	3
18	36	32.0	31.75	32.0
	40	32.0	32.0	32.5
	44	33.0	33.5	33.25
	48	33.0	33.5	33.75
21	36	22.75	22.75	23.0
	40	23.5	23.25	23.25
	44	23.75	23.5	23.5
	48	23.75	23.5	26.0
24	36	17.25	17.5	17.75
	40	17.25	18.0	18.25
	44	18.25	18.25	18.5
	48	18.5	19.0	19.0

Table 4.4 ANOVA of the effects of T and S on incubation period for *P. auratus* eggs at temperatures of 18, 21 and 24^{0}C and salinities of 36, 40, 44 and 48‰.

Source	DF	SS	MS	F	Prob
Model	3	1283.86	427.95	403.88	< 0.001
Error	32	33.91	1.06		
Total	35	1317.77			
Effect test					
T	1	12.12		11.44	0.0019
S	1	0.47		0.44	0.5103
T*S	1	0.09		0.08	0.7750

4.3.3 Effect of temperature and salinity on hatching proportion

The percentage of eggs which developed normally was relatively low, ranging from 12.2% to 27.5%, compared to 58% in the reference sample taken at the beginning of the experiment. The ANOVA showed no significant difference between experimental treatments (P = 0.22) (Table 4.5).

Table 4.5 ANOVA results of the effects of T and S on hatching success of *P. auratus* eggs.

Source	SS	DF	MS	F ratio	Prob>F
Model	61.12	11	5.56	1.44	0.22
Error	92.56	24	3.86		
Total	153.67	35			

4.3.4 Effect of temperature and salinity on length at hatch

Viable larvae ranged in length from 1,418 μm to 2,323 μm TL with a mean length of 1,934 μm (Fig. 4.3).

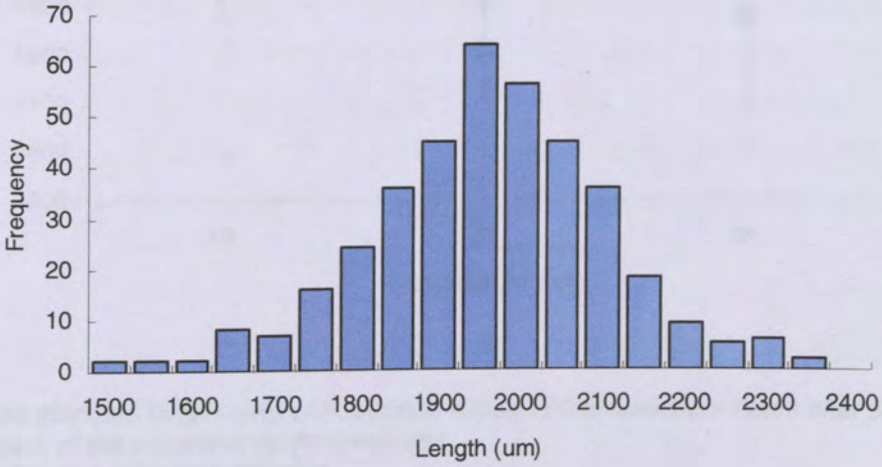


Fig. 4.3 Frequency distribution of the total length of 360 snapper larvae that were sampled 120 temperature-hours after the time of 50% hatch.

Analysis of the effect of temperature and salinity on TL revealed a significant effect of temperature, but no salinity effect or interaction (Table 4.6). Multiple comparisons (Tukey HSD test) indicated that the mean TL was significantly greater at 18^0C than the other two temperatures, but was less at 21^0C than 24^0C (Fig 4.4).

Table 4.6 ANOVA results of the effects of T and S on length of *P. auratus* larvae 120 temperature-hours after 50% hatch (n = 360).

Source	SS	DF	MS	F ratio	Prob>F
Model	2462092	11	223827	11.88	<0.001
Error	6558930	348	18847		
Total	9021022	359			
Effect test					
Temperature	389317	2	194659	10.33	<0.001
Salinity	115642	3	38547	2.05	0.107
Temp*Sal	105264	6	17544	0.931	0.473

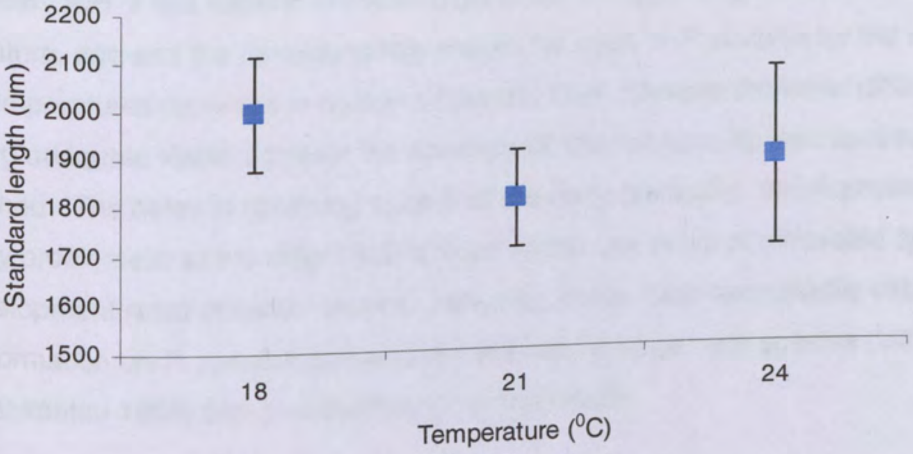


Fig. 4.4 Mean standard length (µm) of P. auratus larvae 120 temperature-hours after 50% hatch at each of the experimental temperatures.
Error bars indicate 1 standard deviation.

4.3.5 Effect of temperature and salinity on larval viability

Larval viability ranged from 65% to 100% across the 36 containers. Although there was a generally lower proportion of viable larvae at 24^{0}C, a two factor ANOVA showed no significant differences (P=0.12) between temperatures or salinities (Table 4.7).

Table. 4.7 ANOVA results of the effects of T and S on the viability of *P. auratus* larvae

Source	SS	DF	MS	F ratio	Prob>F
Model	2,813	11	255.7	1.71	0.12
Error	3,534	24	147.2		
Total	6,347	35			
Effect test					
Temperature	536.1	2	268.1	1.82	0.18
Salinity	96.4	3	32.1	0.22	0.88
Temp*Sal	130.7	6	21.8	0.15	0.99

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4.4 Discussion

The primary aim of this experiment was to generate a relationship between temperature, age and the developmental stages for eggs of *P. auratus* for the range of water temperatures recorded in northern Spencer Gulf. Despite the initial difficulties in obtaining adequate viable eggs for the experiment, the relationship was successfully established. The delay in obtaining eggs until the early blastodisc development stage was only problematic to the extent that it required the use of some simulated data for the development rates at earlier stages. However, these data were readily estimated from information on *P. auratus* (Crossland 1980) and a co-generic species (Mihelakakis and Yoshimatsu 1998) and give confidence in the results.

The rate of development was significantly affected by temperature in the 18 – 24^{0}C range of this study. This is consistent with the findings of many other studies (reviewed in Pauly and Pullin 1988) including those on *P. major* (Apostolopoulos 1976; Mihelakakis and Yoshimatsu 1998). The present study was concerned with the temperature range found in northern Spencer Gulf during the spawning season and did not attempt to identify tolerance limits for the population. Mihelakakis and Yoshimatsu (1998) investigated the development of eggs of *P. major* over a much wider temperature range and reported that the lower and upper temperature tolerances for viable hatch (the hatching of viable larvae) were 13-14^{0}C and 27-28^{0}C respectively. The lower end of the 15-23^{0}C range of natural spawning temperatures for this species in Japan (Mihelakakis and Yoshimatsu 1998) is probably lower than that of the range during the spawning season in northern Spencer Gulf (see Sect. 5.3.1). However, there is also considerable overlap and so the tolerances reported in that study could usefully be used as an indicator of the tolerances for the eggs of *P. auratus.*

Salinities between 36 and 48‰ did not exert a significant influence on incubation period. These salinities exceeded the range recorded during plankton sampling and reported in other studies of northern Spencer Gulf (Bye and Whitehead 1975; Bullock 1975; Nunes and Lennon 1986). Salinity has also been found not to affect the incubation period in other studies of sparid species (Mihelakakis and Kitajima 1994; Mihelakakis and Yoshimatsu 1998), and for other marine species (Walsh et al. 1991). Apostolopoulos (1976), on the other hand, found incubation period decreased with increasing salinities from 11‰ to 35‰ at a given temperature for *P. major.*

The range of T and S investigated in this study had no significant effect on the hatching proportion or larval viability. The more comprehensive study of Mihelakakis and Yoshimatsu (1998) for *P. major* reported that both of these factors were affected by T and S, particularly at levels outside of 12.7 - 28.2^{0}C and 12 - 48‰, where hatching rate was either low or zero. The eggs in the present study suffered from high mortality (and/or poor fertilisation e.g. Battaglene and Talbot 1992) from the beginning of the experiment and the hatching proportion results should therefore be taken with caution. However, it appears that the eggs in the present study showed a greater ability to hatch at 48‰ than the Japanese study. This may reflect the acclimation of the broodstock to the relatively hypersaline ambient water conditions of northern Spencer Gulf compared to the Japanese study where ambient salinities were 29 – 32.5‰ (Mihelakakis and Yoshimatsu 1998). However, the effect of broodstock acclimation on the response of eggs and larvae to different salinities is not consistent, with both positive relationships established (Holt et al. 1981; Freddi et al. 1981; Gray et al. 1991) and no relationship found (May 1975; Lee et al. 1981).

The lack of significant differences in larval viability are consistent with the findings of Mihelakakis and Kitajima (1994) and Mihelakakis and Yoshimatsu (1998) who reported optimum larval viability within the ranges of ambient T and S that are found in the natural distribution of the two sparids considered. Larval viability has been suggested as the best measure of optimum spawning conditions for aquaculture purposes. If that concept is extended to a measure of spawning success in the wild, it would appear that little or no benefit accrues from place of spawning within the study area. A similar conclusion can be drawn from the results of larval lengths. The mean length of 1.9 mm was small compared to the range of 2.1 to 3.1 mm in another study of *P.auratus* where broodstock were hormonally induced, manually stripped of eggs and sperm for fertilisation, and the fertilised eggs incubated at 21.5^{0}C (Battaglene and Talbot 1992). *P. auratus* larvae are at the lower end of larval size at hatch (see review by Miller et al. 1988), with poorly developed eyes, mouth, digestive tracts and motor functions (Pankhurst et al. 1991; Battaglene and Talbot 1992). They are therefore considered "highly susceptible to starvation in periods of sub-optimal prey densities or turbid sea conditions" (Pankhurst et al. 1991). An increase in length at hatch would have inferred a survivorship advantage because of better developed organs, greater yolk mass (Miller et al. 1988). However, an interpretable pattern of temperature and salinity effects was not observed.

The most significant result was the significant reduction in incubation period with increasing temperature. Shorter development times to hatch and then to the development of larval feeding and motor functions infer a decrease in mortality associated with predation and starvation. This may, in part, explain the positive relationship found between recruitment of 1+ juveniles and water temperature recorded in Hauraki Gulf, New Zealand for this species (Francis 1993).

This study successfully described the development of *P. auratus* eggs over a range of temperatures and salinities found in northern Spencer Gulf during the spawning season. The relationship between temperature and age was then used to age snapper eggs collected during the DEPM study described in the following Chapter.

Chapter 5. Use of the Daily Egg Production Method (DEPM) to estimate spawning biomass of *Pagrus auratus* in northern Spencer Gulf.

5.1 Introduction

The Daily Egg Production Method (DEPM) estimates fish spawning biomass by calculating the ratio of daily egg production in the study area to the weight specific daily fecundity of mature fish. The sampling and analytical processes to conduct a DEPM survey were described in detail in an application for the northern anchovy, *Engraulis mordax*, (Lasker 1985). The method has since been in widespread use in clupeoid fisheries (see review by Alheit 1993) but there had been few studies on non-clupeoid species by the mid 1990s (e.g. Koslow et al. 1995). However, the use of DEPM was proposed as a viable method for estimating biomass for three non-clupeoid species, including *Pagrus auratus,* in New Zealand (Zeldis 1993). He based his proposal on the following characteristics of snapper biology:

- Multiple spawners with indeterminate fecundity
- Well defined, daily rhythm of ovulation and spawning
- High spawning frequency
- Well described planktonic eggs

Use of the DEPM requires the collection of plankton and adult fish samples from throughout the study area. The snapper fishery in Hauraki Gulf, New Zealand is a multigear fishery with annual catches exceeding 2,000 t and has a well established research program to support it (Annala et al. 2000). The research program includes trawling as a capture method and a DEPM study of the Hauraki Gulf therefore has the capacity to independently sample adult fish for the reproductive biological parameters that are necessary to estimate. The snapper fishery in northern Spencer Gulf is much smaller and, in spawning season, is largely a single method fishery (handline). Although a trawl fishery for the western king prawn (*Penaeus latisculatus*) operates in the Gulf, it is confined to well established sand & mud trawl grounds and reports few snapper as bycatch (Carrick 1992). This study sought to determine the utility of the DEPM for estimating biomass in a fishery with these constraints.

Specifically, the aims were to:

1) Conduct DEPM surveys to estimate snapper biomass within northern Spencer Gulf by
    a) Sampling pelagic plankton and quantifying snapper egg densities;
    b) Sampling adult snapper to estimate the reproductive parameters of
        i) proportion of spawning females
        ii) sex ratio
        iii) batch fecundity, and
    c) Assess the utility of the method for regular surveys for stock assessment purposes.

5.2 Methods

The method of estimating biomass B followed that of Picquelle and Stauffer (1985):

$$B = \frac{P x A x W x k}{R x F x S} \tag{5.1}$$

where P = daily egg production per unit area (eggs.m^2.day^{-1})
A = spawning area (km^2)
W = average weight of mature female fish (kg)
k = conversion factor (m^2 to km^2, kg to t)
R = sex ratio of mature females to mature fish (by weight)
F = batch fecundity of average weight female
S = proportion of females spawning each day (by weight)

The methods for estimating each parameter are described below.

5.2.1 Egg production (P)

The estimation of total egg production for the study area requires plankton sampling to collect and enumerate egg density.

5.2.1.1 Temporal and spatial sampling considerations

The spawning season for snapper in South Australia had not been well defined. (Jones 1981) reported that "fish were found in spawning condition between October and February..." in Spencer Gulf although the criteria for determining this were not stated. Some quantitative data were available from ovaries collected opportunistically by the author from Port Broughton and Port Neill in central and southern Spencer Gulf respectively in 1991 and 1992. Haemotoxylin and eosin (H&E) stained sections showed vitellogenic and hydrated oocytes between November and February in those years, and the gonadosomatic indices showed peaks in November and December for the two sites (Fig. 5.1). This late spring - summer spawning period is consistent with studies of other southern Australian and New Zealand stocks (Crossland 1977b; Lenanton 1974; Scott and Pankhurst 1992; Zeldis 1993; Coutin 1997).

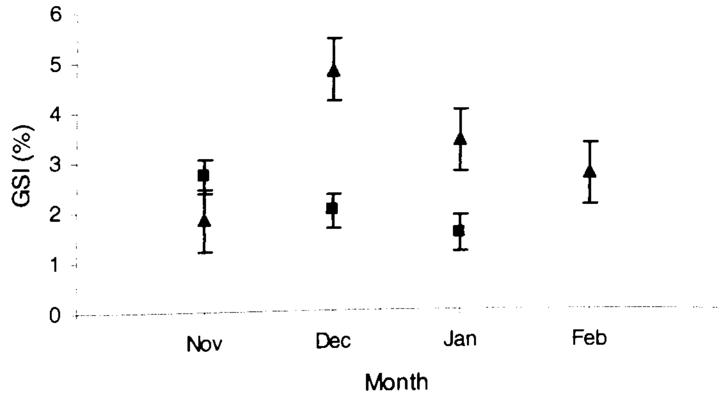


Fig. 5.1 Gonadosomatic indices of snapper from Pt Neill (Δ) and Port Broughton ( ) in Spencer Gulf during 1991 and 1992.

The duration and number of plankton sampling cruises was constrained by the availability of the research vessel *RV Ngerin* to two trips per year and 6-8 days per cruise. Sampling was planned, therefore, to cover the months of assumed spawning over two consecutive years, with a common month each year, and took place in November and December 1994, December 1995 and January 1996. The sampling time within each month was determined by the needs of the adult fish sampling (which occurred concurrently). Most of the adult fish were to be sampled from the handline catches of commercial fishers. Previous sampling experience suggested that these catches were more consistent over neap tides (i.e. little tidal movement) and so the cruises were scheduled to occur at these times.

Sampling time was also limited to approximately 12 hours per day and a decision had to be made as to what hours of each day should be sampled. The calculation of egg production is based on a regression of egg densities against egg age (days) and therefore sampling eggs over a wide range of ages would improve the fit of the regression model. It was assumed that only 0+ and 1+ day old eggs would be sampled given the likely water temperature and its relationship with egg development (Cassie 1956; Crossland 1980; Chapter 4). Therefore, sampling before and after the peak spawning time should yield early 0+ and 1+ day eggs. Other studies have reported peak spawning times from late morning to 1700 hours (Zeldis 1993), 1800 – 1900 hours (Matsuyama et al. 1988) and from sunset into the night (Foscarini 1988). Based on these relatively consistent findings, and without knowledge of the timing in South Australia, sampling was scheduled from approximately 1200 – 2400 hours each day.

There was also no prior knowledge of spatial spawning patterns in Spencer Gulf and, as snapper were caught by commercial fishers throughout Spencer Gulf during the spawning season, sampling was planned to systematically cover the study area (Table 5.1). East-west transects were selected on lines of latitude that were 5 nautical miles apart and sampling stations were spread evenly along each transect. The area represented by each station was calculated by dividing the east – west distance equally between stations and multiplying it by half the distance between the transects to the north and south.

Table 5.1 Characteristics of the 38 sampling stations for *P. auratus* eggs in 1994 and 1995/6.

Station number	Latitude S	Longitude E	Water depth (m)	Area represented (km^2)
1	33^0 59’	137^0 40’	22	328.5
2	34^0 00’	137^0 00’	17	290.4
3	33^0 59’	137^0 20’	11	332.5
4	33^0 54’	137^0 45’	17	278.4
5	33^0 55’	137^0 05’	12	284.3
6	33^0 55’	137^0 24’	19	307.1
7	33^0 50’	137^0 54’	20	278.9
8	33^0 50’	137^0 15’	15	273.8
9	33^0 50’	137^0 34’	15	197.9
10	33^0 45’	137^0 59’	6	122.9
11	33^0 44’	137^0 10’	7	145.7
12	33^0 44’	137^0 20’	15	133
13	33^0 45’	137^0 30’	7	268
14	33^0 40’	137^0 20’	11	201.1
15	33^0 40’	137^{0}30’	11	141.3
16	33^0 40’	137^0 40’	7	191.5
17	33^0 35’	137^0 25’	12	211.1
18	33^0 35’	137^0 36’	13	143.6
19	33^0 35’	137^0 44’	13	195.2
20	33^0 29’	137^0 30’	26	247.7
21	33^0 29’	137^0 40’	15	301.8
22	33^0 24’	137^0 26’	10	128.4
23	33^0 24’	137^0 35’	18	132.9
24	33^0 24’	137^0 44’	6	200.8
25	33^0 20’	137^0 29’	20	238.1
26	33^0 19’	137^0 40’	10	179.4
27	33^0 00’	137^0 30’	25	141.4
28	33^0 15’	137^0 39’	12	206.9
29	33^0 09’	137^0 35’	11	196.8
30	33^0 09’	137^0 46’	9	229.9
31	33^0 04’	137^0 40’	13	172.5
32	33^0 04’	137^0 49’	7	231.1
33	33^0 00’	137^0 44’	11	134.7
34	32^0 58’	137^0 53’	7	158.3
35	32^0 52’	137^0 50’	20	90.38
36	32^0 48’	137^0 50’	9	94.86
37	32^0 42’	137^0 48’	8	199.2
38	32^0 56’	137^0 47’	4	57.8

5.2.1.2 Sampling equipment

Egg samples were collected by towing paired plankton nets of 70 cm diameter and 3 m length behind the *RV Ngerin*. At the time of this sampling, no other studies had quantitatively sampled snapper eggs and so information on appropriate mesh size to use in the codends of the plankton nets was not available. For the first cruise, different mesh sizes were used in each net – 363 μm and 500 μm. After the cruise, the diameter of 100 randomly chosen eggs was measured from each mesh size from each of three sampling stations. The size distributions of these eggs were then compared to assess the relative efficiency of each mesh size (Fig. 5.2). The eggs of *P. auratus* are approximately 0.7 – 0.95 mm in diameter when spawned (Cassie 1956; Crossland 1977b; Scott et al. 1993). The size distributions of eggs in from both mesh sizes were very similar at each station. It was concluded, therefore, that was suitable for capturing snapper eggs and would reduce the amount of sorting compared to 363 μm. As such, the 500 μm mesh was used for all sampling after November 1994.

5.2.1.3 Plankton sampling

Plankton sampling was conducted by an oblique tow of the paired nets from the seabed to the surface. The nets were fitted with an underwater depth gauge that recorded the maximum depth to which they had been deployed. After retrieval, the depth recorded by the gauge was compared to that showing on the ship's depth meter to ensure that the water column had been properly sampled. The plankton samples were stored in 1 l plastic containers and were preserved in a 5% formalin seawater solution for later sorting in the laboratory.

A General Oceanics 2030 R flowmeter was attached to each plankton net and readings were recorded for each net at each sampling station and later converted to volume of water filtered. Data on seawater temperature and depth were recorded from the *RV Ngerin*'s instruments, with the temperature sensor located on the ship's keel about 2m below sea surface.

Two different methods were used to measure water salinity. In 1994, a temperature / salinity profile was taken using a Seabird SBE-19 CTD at a number of stations. The CTD was deployed vertically between the seabed and vessel, with data captured every 2 metres of depth. Subsequent analysis of the CTD measurements showed a well mixed water column with little evidence of stratification (see Results) and the CTD was therefore not used on the 1995/6 cruises. A sample of surface water was taken at each site, stored in a glass bottle and the salinity at each station was calculated later in the laboratory using a Yeo-kal inductively coupled salinometer.

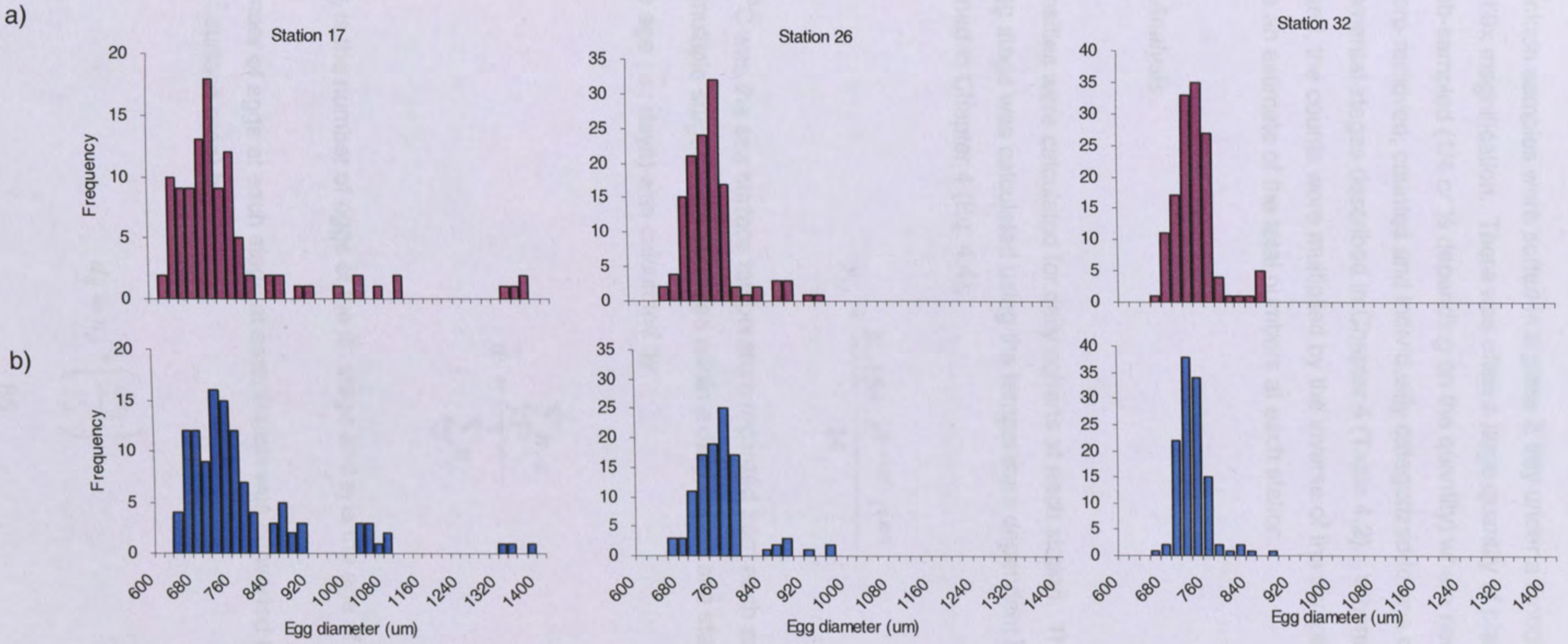


Fig. 5.2 Comparison of the diameters of 100 randomly selected eggs captured with a) 363 μm and b) 500 μm mesh plankton nets at three different stations in northern Spencer Gulf.

5.2.1.4 Laboratory procedures

The plankton samples were sorted in a glass Z tray under a binocular microscope at 100 – 160x magnification. There was often a large quantity of plankton and samples were sub-sampled (1/4 or ½ depending on the quantity) where necessary. Snapper eggs were removed, counted and individually categorized to one of the 16 developmental stages described in Chapter 4 (Table 4.2). Where sub-sampling had been used, the counts were multiplied by the inverse of the sampling fraction to produce an estimate of the total numbers at each station.

5.2.1.5 Analysis

Egg densities were calculated for daily cohorts at each station. The age (hours) of each egg stage was calculated using the temperature dependent development rate determined in Chapter 4 (Eq. 4.4);

$$y_{i,t} = \frac{36.158 \,.\, e^{(-0.12t)}\, i^{0.827}}{24} \tag{5.2}$$

where t^0C was the sea surface temperature recorded from each sampling station. Where multiple stages were recorded within a daily cohort at a station, a weighted average age ($\bar{a}$; days) was calculated by

$$\bar{a} = \frac{\sum_{j=1}^{j} n_j a_j}{\sum_{j=1}^{j} n_j} \tag{5.3}$$

where n_j is the number of eggs of the jth stage and a_j is the age of the jth stage egg.

The number of eggs at each stage at each station was converted to egg density (d_{ij}; eggs.m^{-2} surface area) by

$$d_{ij} = n_{ij} * \left(\frac{de_j}{v_j} \right) \tag{5.4}$$

where n_{ij} = number of ith stage eggs at station j

de_j = depth sampled at station j (m)

v_j = volume of water filtered at station j (m^3)

Daily egg production (P) was estimated by fitting a non-linear least squares regression to the density of eggs against their age in days. The non-linear model used was

$$P_{jk} = P_0\, e^{(-Z\, t_{jk})} + \varepsilon_{jk} \tag{5.5}$$

(Picquelle and Stauffer 1985)

where P_{jk} = the number of eggs in day k from station j

P_0 = daily egg production per unit area

Z = the daily instantaneous rate of egg mortality

t_{jk} = the age in days of eggs of cohort k at station j

Confidence intervals for P were calculated using non-parametric bootstrapping methods (Manly 1997). Computer facilities were not available to repeatedly re-run non-linear regressions after re-sampling and so the data were first log transformed and a linear regression conducted to estimate $\ln P$. $\ln P$ was antilogged to P by

$$P = e^{\left(\ln P + \frac{s^2}{2}\right)} \tag{5.6}$$

(Picquelle and Stauffer 1985)

where s^2 is the regression mean square error. This process was repeated 1000 times and the 95% confidence intervals were taken directly from the bootstrap distribution of P (simple percentile CI; Manly 1997). All bootstrapping in this study was undertaken using the Resampling Stats add-in developed for MS Excel (Blank et al. 2001).

5.2.2 Adult parameters

Collection of data from mature snapper was conducted concurrently to the plankton sampling in each month. One research team was stationed on each side of Spencer

Gulf with the objective of working with local commercial and recreational fishers to collect data from their catches. Data were collected for length, weight, sex and reproductive condition.

5.2.2.1 Sex ratio (R) and proportion of mature females spawning (S)

For each landing, individual fish were measured (cm LCF) and weighed whole (0.1 kg for larger fish and 1g for fish < 1kg). The fish were then eviscerated and the sex recorded. The ovaries were removed from female fish and staged macroscopically following (Scott et al. 1993). Each ovary was separately weighed (0.01g) when they were classified as vitellogenic, hydrated or ovulated. A small section was cut from the centre of one ovary, placed in a histology cassette and fixed in a 10% formalin seawater solution for later histological (H&E) staining.

Prior to the DEPM sampling, an analysis of the distribution of oocytes within and between the ovaries had been conducted. The sample fish (350 cm LCF) had been caught in southern Spencer Gulf and was macroscopically staged as hydrated. Sections were cut from the anterior and posterior parts of both ovaries. Oocytes and connective tissue were carefully cut from the epithelium and teased apart in water in a petri dish using fine forceps. A sample of 200 oocyte diameters were then measured along a random transect across the petri dish using the image analysis software Video Pro. The distributions of oocyte diameters (Fig. 5.3) were compared using a single factor (location) ANOVA. No significant difference was found between the ovary segments ($P = 0.19$) and so the sampling location was standardised at the centre of either ovary.

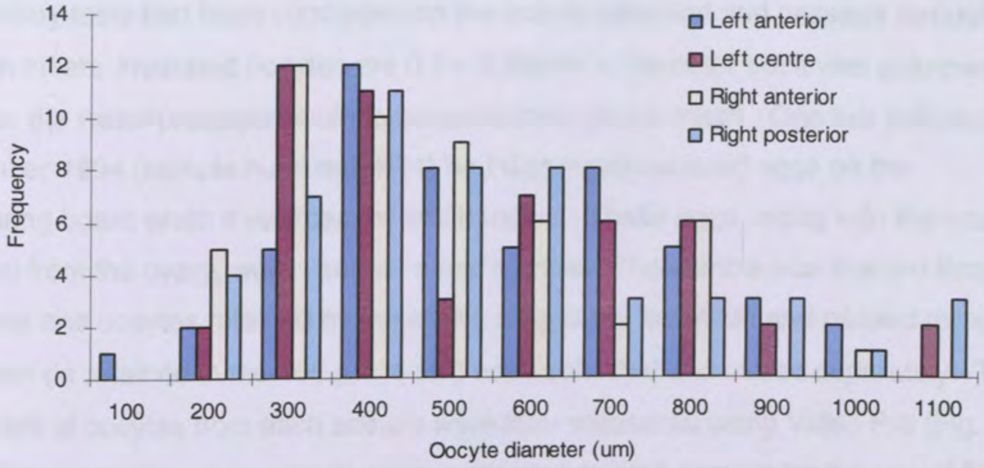


Fig. 5.3 Distribution of 200 oocyte diameters from different locations on the ovaries of a single P. auratus.

Females were categorised as spawners or non-spawners from the stage of oocyte development evident in the stained ovary sections – either by the presence of hydrated oocytes or by post-ovulatory follicles (POF) depending on the time of capture. Snapper are daily spawners with discrete batches of oocytes undergoing vitellogensis, hydration, ovulation and spawning each 24 hour period (Matsuyama et al. 1987; Matsuyama et al. 1988; Scott et al. 1993). Sections of ovary from mature fish captured during the morning showed oocytes in late stage vitellogenesis or hydration. For fish captured in the late evening or night, ovary sections showed POFs and oocytes at the migratory nucleus stage (indicative of the next batch of oocytes to be spawned).

5.2.2.2 Batch fecundity

The second ovary of each fish was stripped of oocytes using the methods described by (Lowerre-Barbieri and Barbieri 1993). The ovary was cut open longitudinally and oocytes detached from the epithelium and connective tissue using water pressure. The oocytes were collected in a sieve constructed from 100 mm water pipe in which two separate, sequential filters were placed – an initial 500 μm mesh followed by a 100 μm second mesh. The oocyte samples were collected from the 500 μm mesh and preserved in a 2% formalin seawater solution for later analysis in the laboratory.

Preliminary tests had been conducted on the oocyte retention and passage through the 500 µm mesh. Hydrated oocytes are 0.7 – 0.95mm in diameter but it was unknown whether the water pressure would force some through the mesh. One fish collected in November 1994 (sample number GE14) had disgorged ovulated eggs on the measuring board when it was caught and handled. These eggs, along with the oocytes stripped from the ovary, were used as a test sample. The sample was flushed through the sieve and oocytes retained by the mesh, clogged in the mesh and passed through the mesh (ie retained in the 100 µm mesh) were collected and stored separately. The diameters of oocytes from each sample were later measured using Video Pro (Fig. 5.4). The separation of oocytes in each category provided support for the use of 500 µm mesh to collect hydrated oocytes.

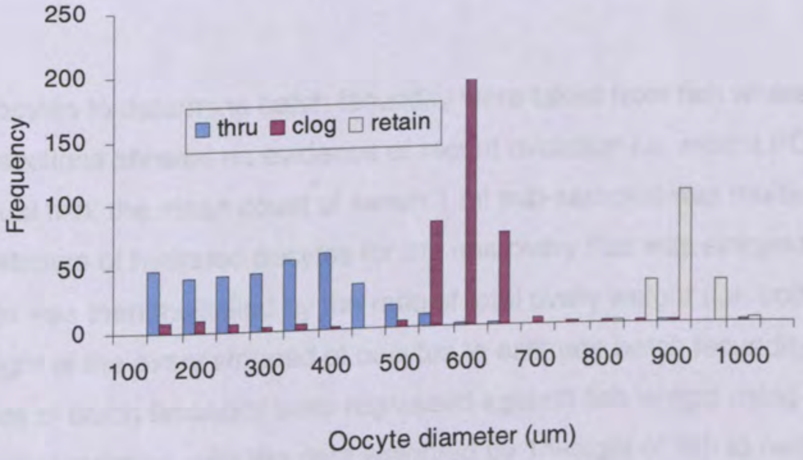


Fig. 5.4 Frequency distribution of the diameters of the oocytes of P. auratus that passed through, clogged in the mesh of or were retained by a 500 µm sieve under water pressure.

Batch fecundity was likely to range from approximately 8,000 to 140,000 (Crossland 1977a) and a method of volumetric sub-sampling was developed to reduce laboratory time. The ovulated eggs from fish GE14 were again used to develop this method. 10,000 oocytes were counted and placed in a 2% formalin solution in 500 ml of tapwater. The eggs were stirred and a 1 ml sub-sample was drawn from the solution. The oocytes were counted and then returned to the solution. This was repeated ten times and a running mean and standard error calculated (Fig. 5.5). The trial was repeated for a second set of ten sub-samples. These trials suggested that a mean count of seven sub-samples per fish would yield an estimate of batch fecundity with a CV (SE/mean) of < 8%.

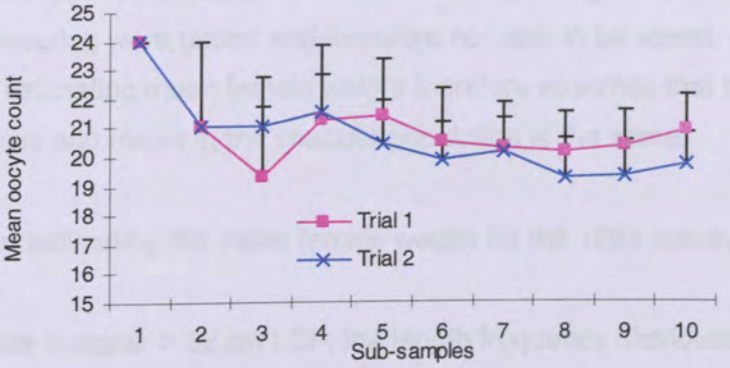


Fig. 5.5 Running mean of oocyte counts taken from 1 ml sub-samples of a 500 ml solution of 10,000 ovulated snapper oocytes. The error bars are SE.

Counts of oocytes to determine batch fecundity were taken from fish where the histological sections showed no evidence of recent ovulation i.e. recent POFs. For each individual fish, the mean count of seven 1 ml sub-samples was multiplied by 500 to give an estimate of hydrated oocytes for the one ovary that was stripped of oocytes. This estimate was then multiplied by the ratio of total ovary weight (i.e. both ovaries) over the weight of the ovary stripped of oocytes to estimate batch fecundity for the fish. The estimates of batch fecundity were regressed against fish weight using least squares linear regression, with the data weighted by 1/weight of fish to remove the dependence of the variance on the mean (Zeldis & Francis 1998). The batch fecundity of the mean weight of a mature female snapper was later calculated from the regression relationship.

5.2.2.3 Mean female weight (W)

The mean weight of mature female fish is generally calculated from a number of independent samples taken during the DEPM surveys. However, in this study, sampling difficulties limited the number of samples in absolute numbers, and in the geographic range and capture method of those samples. Furthermore, the minimum legal length for snapper (≈32cm LCF) exceeds the size at first maturity of ≈23cm LCF

(Crossland 1977a; Zeldis and Francis 1998); this study) and so fishery dependent samples did not fully reflect the size structure of the mature biomass. Average female weight was therefore calculated from an analysis of the market measuring data collected for the age structure study (Chapter 3), with an adjustment made for fish between the size at first maturity and the minimum legal length. The fish measured in the market measuring were gutted and therefore not able to be sexed, and the use of these data for estimating mean female weight therefore assumes that the average weight of females and males in the snapper population is the same.

The process for estimating the mean female weight for the 1994 surveys was as follows:

1) For legal size snapper > 32 cm LCF, the length frequency distributions collected during the market measuring survey for the October - December 1994 period (see Fig. 3.4) were used for both the November and December 1994 calculations.
2) For mature snapper < 32 cm LCF, the age length keys from Cnapter 3 suggested would be comprised of a proportion of 2+ and 3+ snapper. To add the contribution of 3+ fish to spawning biomass,
    a) The mean size was estimated for fish at the age of 3.9 years, which approximates the mid-point between November and December 1994. The mean size was estimated as 32.7 cm LCF from the generalised von Bertalanffy growth curve (see Chapter 7; Eq. 7.2 and Table 7.3). This closely aligned with the legal minimum length and therefore the cutoff of the market measuring size distribution, and meant that only the left side of the 3+ distribution needed to be added.
    b) The standard deviation of the size distribution of 3+ snapper was estimated from the research sampling and market measuring samples of this age class, and determined as 5.18 cm (Fig. 5.6).

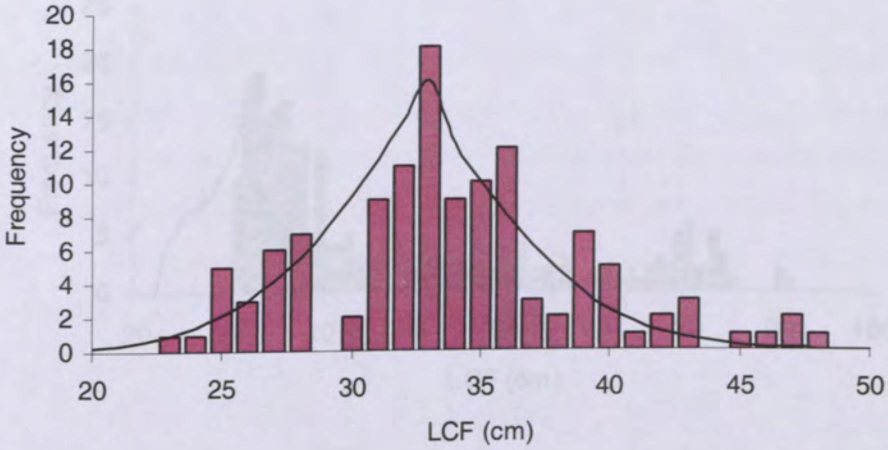


Fig. 5.6 Size frequency of 3+ snapper from market measuring and research sampling with a normal distribution (mean 32.7, SD 5.16 cm) overlaid.

3) To add the contribution of 2+ snapper to mean weight, step 2a) was repeated for 2.9 year old fish and showed a mean size of 25.0 cm LCF. Inadequate data were available to calculate the SD of 2+ fish and so the relative magnitude of the SD for 3+ was used and gave a SD of 3.95 cm. The size distribution of 2.9 year old fish extended <23 cm LCF and so the distribution of these fish was truncated at that size.

The left hand side of the 3+ size distribution was added to the market measuring sample with a magnitude equal to the peak of the measured sample (Fig. 5.7). No relative yearclass strength data were available for the 2+ yearclass but, as strong consecutive yearclasses were not common, the 2+ yearclass was added with a magnitude ½ of the 3+ yearclass (Fig. 5.7). Weights for each size class were calculated from the length-weight relationship established in this study (see Results). The weight samples were bootstrapped 1,000 times and the 2.5% and 97.5 % confidence intervals taken directly from the bootstrap distribution (Manly 1997).

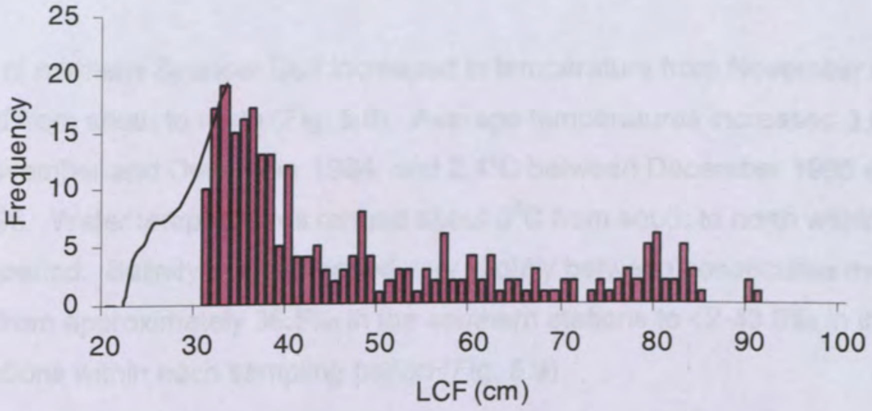


Fig. 5.7 Size frequency of snapper measured during October – December 1994. The solid line shows the simulated size distribution for 2+ and 3+ fish at lengths below the legal minimum length.

To estimate the average weight of female fish for the 1995 / 96 DEPM surveys, a new length frequency distribution was derived by 1) re-calculating the length 1 year later for each length class using Eq 7.2, and 2) recalculating weight at length for each new length class. Confidence intervals were again bootstrapped.

5.2.3 Biomass estimates

Spawning biomass was estimated using Eq. 5.1. The 95% confidence intervals were taken directly from 1,000 bootstrap estimates of B calculated using the 1,000 bootstrap estimates of P, W, R, *and* S. The 1,000 estimates of batch fecundity, F were calculated from the regression equation relating batch fecundity to weight and using each bootstrap estimate of W.

5.3 Results

This study has produced information on the water temperature and salinity in northern Spencer Gulf at the time of the snapper season, as well as biological information on the distribution of snapper eggs and the reproductive status of adult snapper.

5.3.1 Plankton sampling sites

The waters of northern Spencer Gulf increased in temperature from November through January and from south to north (Fig. 5.8). Average temperatures increased 3.0°C between November and December 1994, and 2.1°C between December 1995 and January 1996. Water temperatures ranged about 3°C from south to north within any one survey period. Salinity only increased very slightly between consecutive months but ranged from approximately 36.5‰ in the southern stations to 42-43.5‰ in the northern stations within each sampling period (Fig. 5.9).

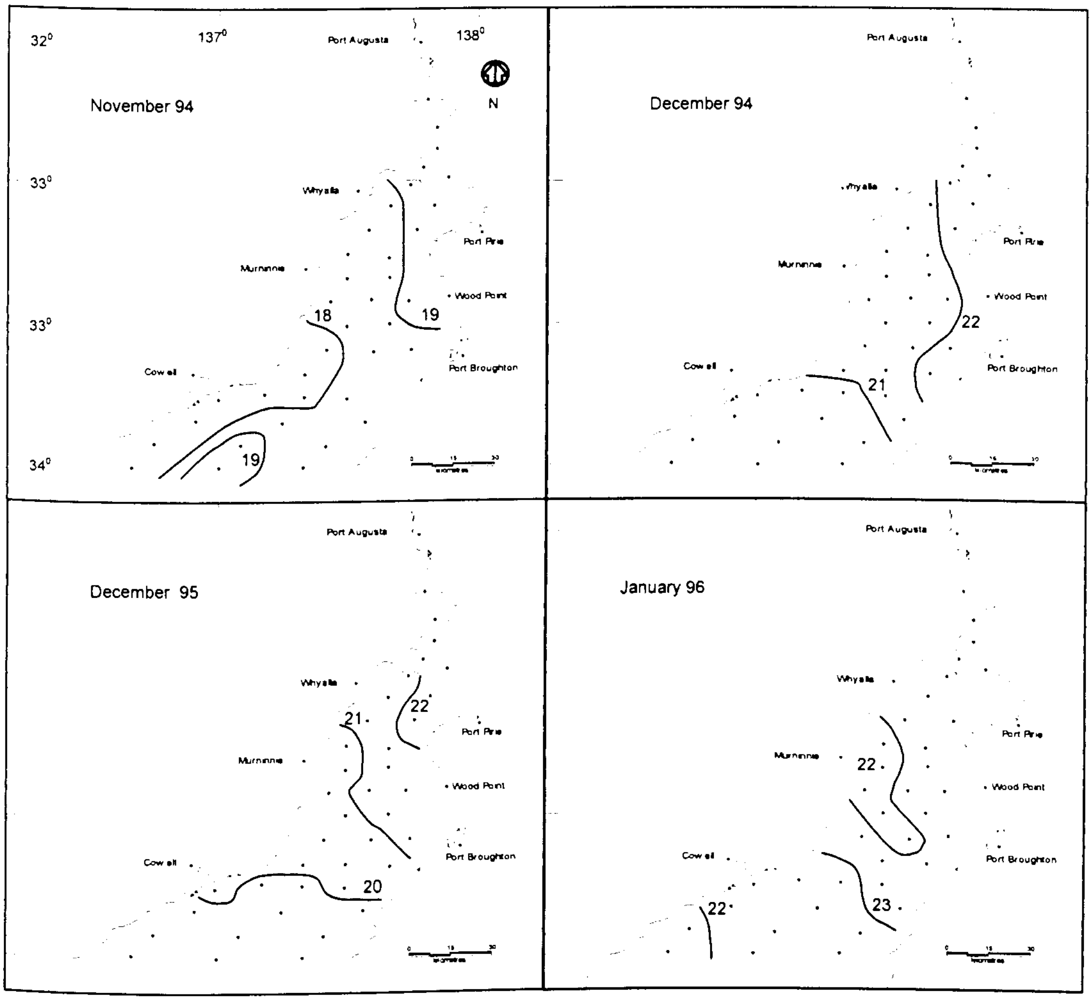


Fig. 5.8 Surface water temperature during the four sampling periods in a) November 1994, b) December 1994, c) December 1995 and d) January 1996

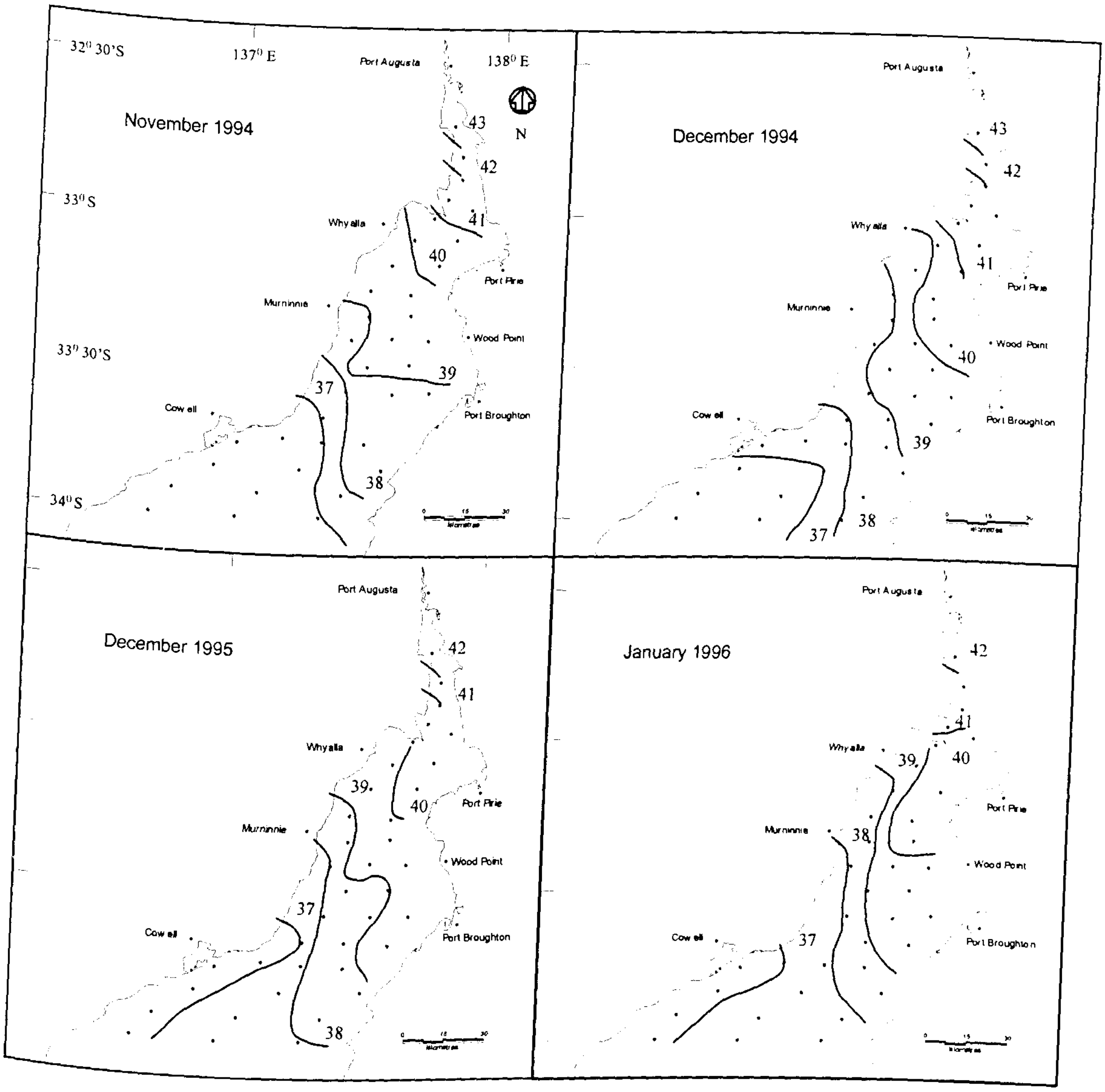


Fig. 5.9 *Salinity during the four sampling periods in a) November 1994, b) December 1994, c) December 1995 and d) January 1996*

The water column was generally well mixed with little evidence of a well defined thermocline (Fig. 5.10), indicating that the near surface samples and measurements taken during 1995/6 satisfactorily represent the water conditions at that site. Water temperature varied up to 0.5°C and salinity varied < 0.5‰.

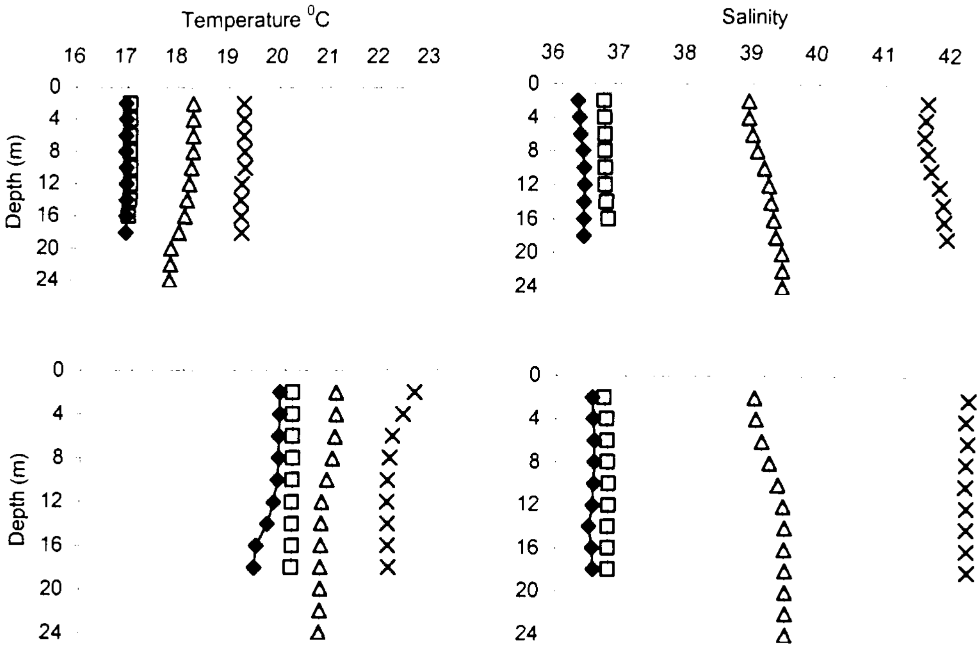


Fig. 5.10 Temperature and salinity profiles of four stations in top) November 1994 and bottom) December 1994. In each graph, Stations 1, 7, 20 and 35 read from left to right.

5.3.2 Egg samples

The collection of snapper eggs provided information on the spatial and temporal patterns of the spawning of snapper in northern Spencer Gulf, and allowed estimation of total egg production and the back-calculation of median daily spawning times.

5.3.2.1 Egg distribution and densities

The number of snapper eggs was greater in December 1994 than November 1994 and in December 1995 than January 1996, suggesting that December may be the peak spawning time in this region. The December samples showed greatest abundances in the central region of northern Spencer Gulf with few eggs north of Port Pirie or south of Cowell (Fig. 5.11). But the distribution pattern amongst stations was not consistent between years. Egg densities ranged from 0 to 83 eggs.m^{-2}.

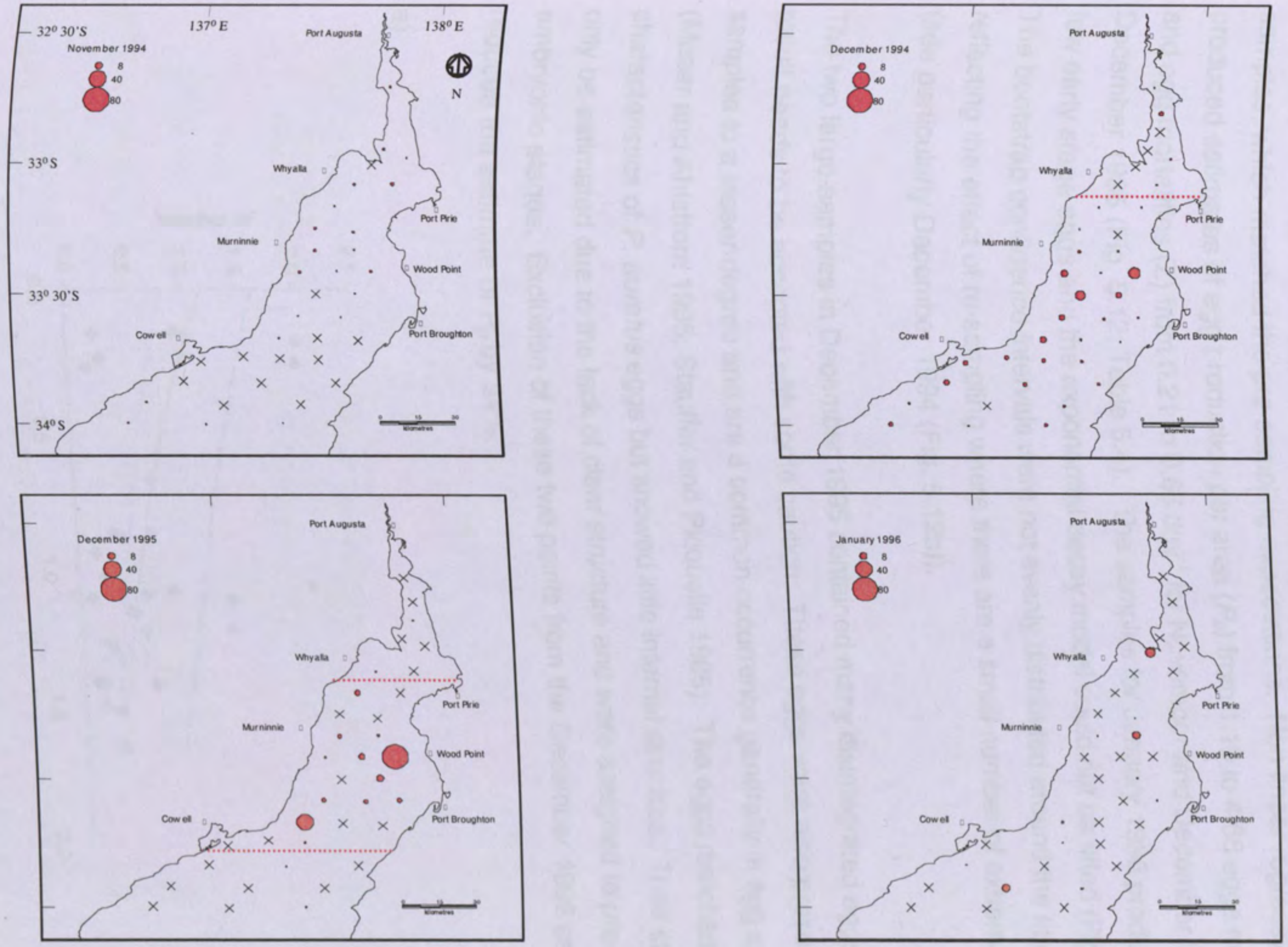


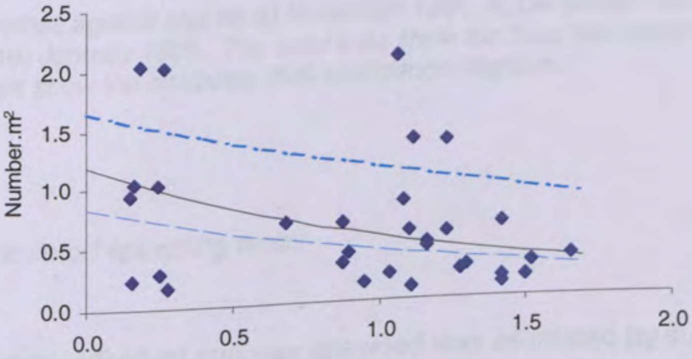
Fig. 5.11 Density of P. auratus eggs of (eggs.m^{-2}) in northern Spencer Gulf in a) November 1994, b) December 1994, c) December 1995 and d) January 1996. No eggs were recorded at stations marked with x. The red dotted lines in the December charts show the spatial boundaries for the biomass estimates.

5.3.2.2 Egg production

The strategy of sampling between midday and midnight worked well in relation to capturing eggs of 0+ and 1+ eggs in all months except January 1996 where few 0+ eggs were recorded (Fig. 5.12). Few eggs of ages 7 – 20 hours were captured in any samples, which matched the pre-sampling expectations. Non-linear regressions produced estimates of egg production per area (P_0) from 1.19 to 4.68 eggs.m^{-2}.day^{-1} and egg mortalities (Z) from 0.21 to 0.66 day^{-1} for November and December 1994 and December 1995 (Fig. 5.12; Table 5.4). The samples for January 1996 produced very few early stage eggs and the exponential decay model could not be fitted (Fig. 5.12d). The bootstrap confidence intervals were not evenly distributed around the fitted lines, reflecting the effect of re-sampling where there are a small number of extreme values (see particularly December 1994 (Fig. 5.12b)).

The two large samples in December 1995 contained many disintegrated eggs and this result needs to be accepted with some caution. These eggs were also present in other samples to a lesser degree and are a common occurrence generally in egg sampling (Moser and Ahlstrom 1985; Stauffer and Picquelle 1985). The eggs matched the characteristics of *P. auratus* eggs but showed little internal structure. Their stage could only be estimated due to the lack of clear structure and were assigned to pre-embryonic stages. Exclusion of these two points from the December 1995 sample reduced the estimate of P_0 by 34%.

a)



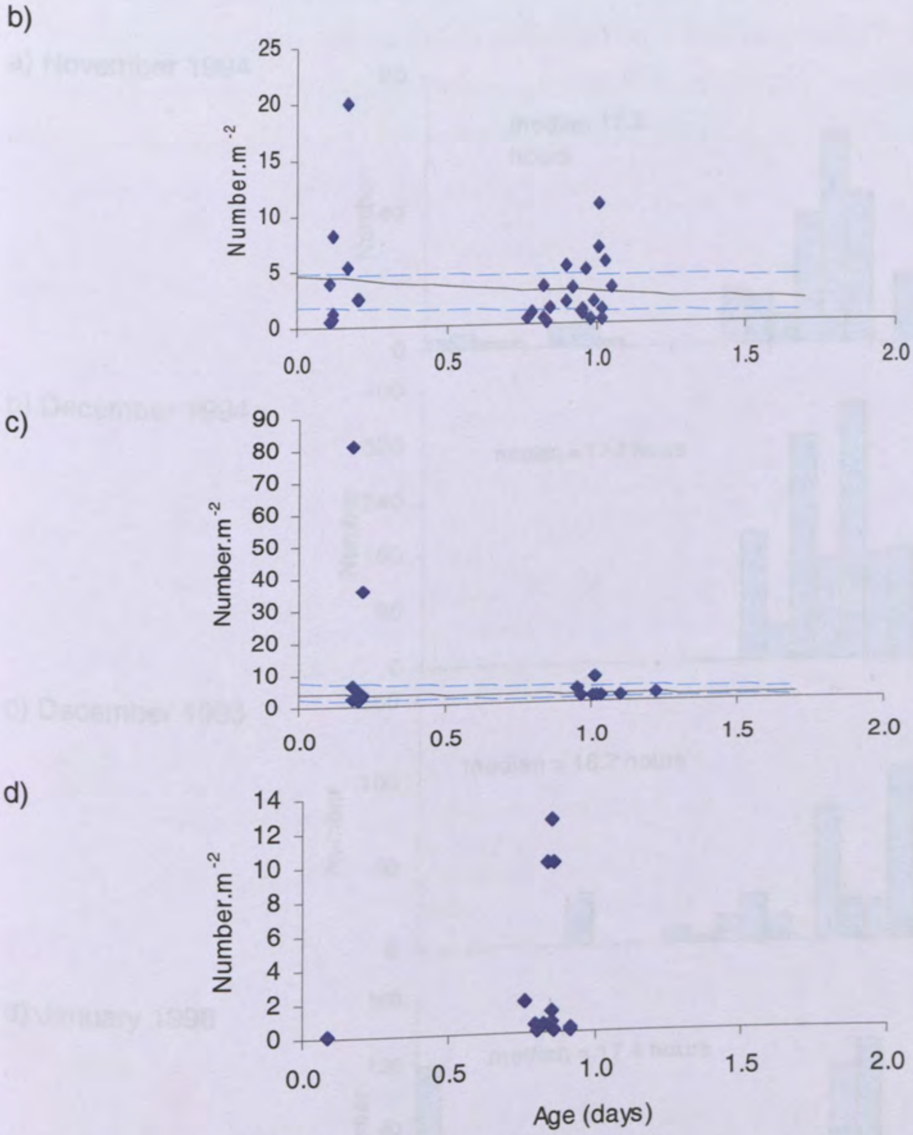


Fig. 5.12 Egg densities against age for a) November 1994, b) December 1994, c) December 1995 and d) January 1996. The solid lines show the fitted non-linear regression and the dotted lines show the bootstrap 95% confidence intervals.

5.3.2.3 Back-calculated spawning times

The time when each individual egg was spawned was estimated by subtracting the estimated age of the egg from the time of day it was sampled (Fig. 5.13). Median spawning times were very consistent between sampling months and ranged from 17.3 – 18.7 hours in the late afternoon. These data suggested some isolated spawning at most times of the day, but was most common from 1400 to 2400 hours.

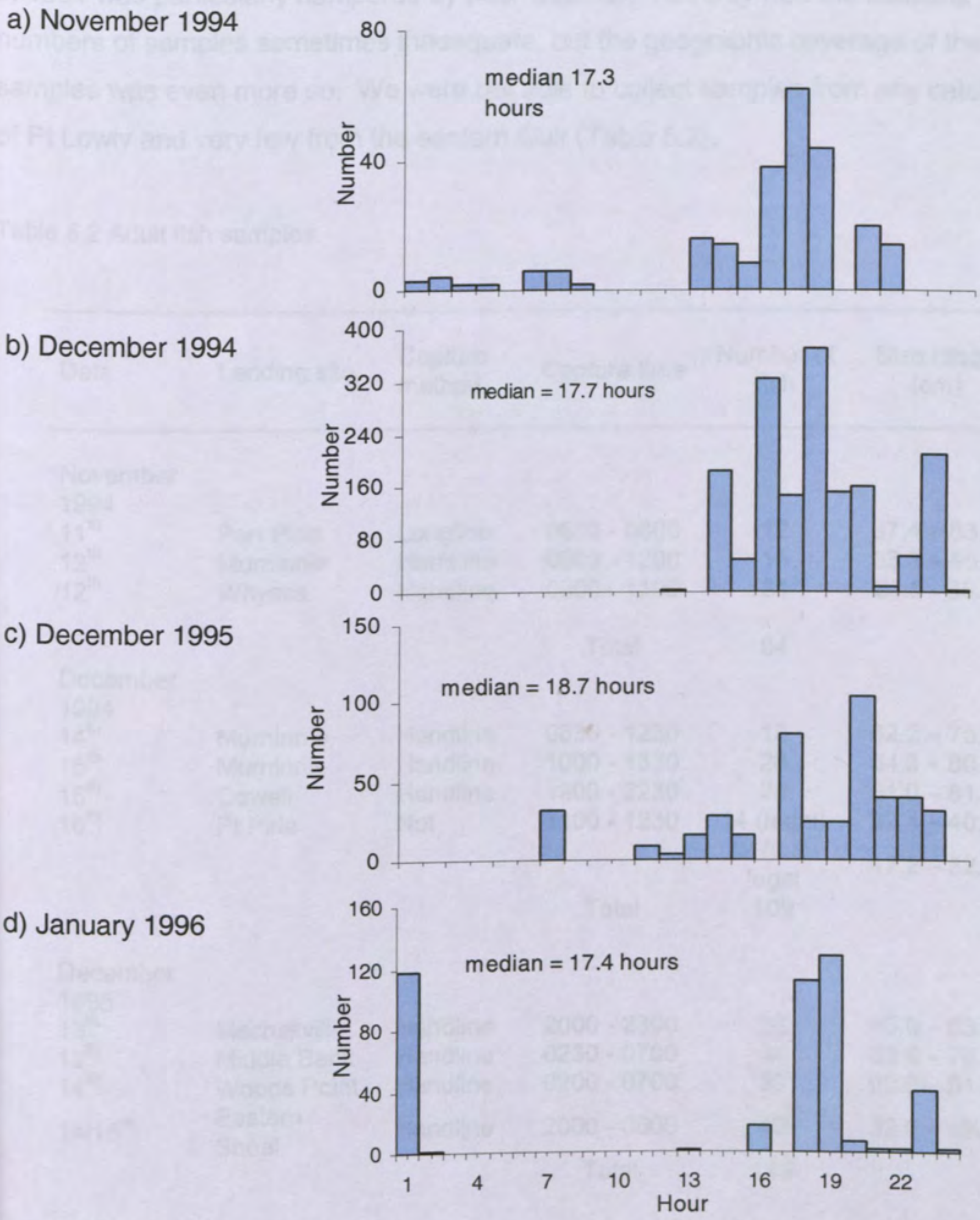


Fig. 5.13 Back-calculated spawning times for each sampling period.

5.3.3 Adult parameters

Collection of adequate adult samples proved problematic, particularly on the first three surveys. The samples were generally collected from the normal catches of commercial fishers and the activity of these fishers is heavily weather dependent due to the relatively small vessels that they work from. The activity of fishers during the surveys in 1994 was particularly hampered by poor weather. Not only was the absolute numbers of samples sometimes inadequate, but the geographic coverage of the samples was even more so. We were not able to collect samples from any catch north of Pt Lowly and very few from the eastern Gulf (Table 5.2).

Table 5.2 Adult fish samples

Date	Landing site	Capture method	Capture time	Number of fish	Size range (cm)
November 1994					
11th	Port Pirie	Longline	0600 - 0800	12	37.4 – 83.7
12th	Murninnie	Handline	0600 - 1200	18	33.3 – 85.4
12th	Whyalla	Handline	0900 - 1100	34	23.5 - 85.2
			Total	64	
December 1994					
14th	Murninnie	Handline	0830 - 1230	18	32.2 – 75.8
15th	Murninnie	Handline	1000 - 1330	28	34.3 – 80.0
16th	Cowell	Handline	1900 - 2230	25	31.0 – 81.7
16th	Pt Pirie	Net	1100 - 1230	14 (legal)	32.4 – 40.1
				32 (sub-legal	17.2 – 32.3
			Total	109	
December 1995					
13th	Mitchellville	Handline	2000 - 2300	26	40.0 – 83.5
13th	Middle Bank	Handline	0230 - 0700	44	32.5 – 78.5
14th	Woods Point	Handline	0200 - 0700	30	32.6 – 51.2
14/15th	Eastern Shoal	Handline	2000 - 0600	49	32.8 – 49.5
			Total	149	
January 1996					
14th	Whyalla	Handline	0400 - 1000	27	31.5 – 46.5
15th	Mitchellville	Handline	1930 - 2330	25	35.5 – 82.1
15th	Mitchellville	Handline	0800 - 1200	37	33.5
15th	Murninnie	Handline	1100 - 1700	60	31.4 – 84.6
16th	Murninnie	Handline	1600 - 2000	92	32.4 – 64.5
17th	Murninnie	Handline	1000 - 1600	52	31.6 – 68.8
17th	Mitchellville	Handline	2030 - 2300	8	28.7 – 37.0
17th	Mitchellville	Handline	2030 - 2300	12	33.0 – 86.7
17th	Pt Pirie	Net	0845 - 0930	30	47.5 – 94.5
18th	Murninnie	Handline	0700 - 1330	20	33.0 – 74.5
			Total	363	

5.3.3.1 Size at first maturity, sex ratio and spawning frequency

The size at first maturity has been reported as 23 cm LCF in New Zealand (Zeldis and Francis 1998) and 22cm LCF for fish captured east of Moreton Island, Queensland (Ferrell and Sumpton 1997). An assessment of the size at first maturity was not an objective of the present study but some samples of small snapper were collected. The results appear consistent with both other studies with 50% maturity at 22-24 cm LCF (Fig. 5.14), although the sample sizes for the critical size classes of 21, 22 and 23 cm LCF were all small (n = 1), and so these results are not reliable. But other size classes had sample sizes of ≥ 3 and so can be treated with more confidence. With no evidence to the contrary, and to maintain some consistency with the other temperate studies of New Zealand, it was assumed that 23cm LCF is the size at first maturity.

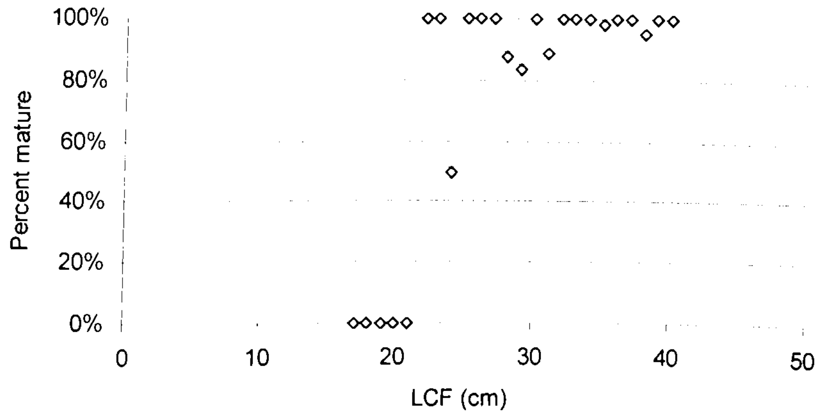


Fig. 5.14 Percent maturity of female snapper captured in northern Spencer Gulf during November and December 1994, December 1995 and January 1996.

Sex ratios were generally close to 50% by number and slightly higher by weight (Table 5.3). The proportion of female snapper spawning showed substantial geographic variation (Table 5.3). Samples taken from north of latitude 33.30^{0}S (eg Whyalla, Port Pirie, Woods Point and Eastern Shoal) showed very low spawning proportions whereas those from the south-eastern regions (Merninnie and Cowell) were much higher. This is broadly consistent with the distribution pattern of eggs (Fig. 5.11). The geographic variation in spawning proportion presented a problem for the DEPM analyses as the method assumes spatial consistency in parameters.

Table 5.3 Sex ratio (proportion F to M)and proportion of females spawning by number and weight

Date & location	Sex ratio (F:M) number	Sex ratio (F:M) weight	Spawning frequency of females number	Spawning frequency of females weight
November 1994				
Port Pirie	0.33	0.40	0.25	0.31
Merninnie	0.58	0.74	0.7	0.73
Whyalla	0.65	0.37	0.05	0.06
Weighted mean	0.49	0.58	0.75	0.58
December 1994				
Murninnie	0.59	0.46	0.40	0.66
Murninnie	0.43	0.73	0.39	0.7
Cowell	0.56	0.52	0.93	0.98
Pt Pirie	0.5	0.48	0	0
Weighted mean	0.52	0.53	0.60	0.69
December 1995				
Mitchellville	0.71	0.74	1.0	1.00
Middle Bank	0.36	0.45	0.69	0.79
Woods Point	0.66	0.72	0	0.00
Eastern Shoal	0.51	0.52	0.04	0.04
Weighted mean	0.53	0.64	0.62	0.72
January 1996				
Whyalla	0.48	0.47	0	0
Mitchellville	0.44	0.38	0.91	0.91
Mitchellville	0.57	0.57	1	1
Murninnie	0.4	0.37	0	0
Murninnie	0.42	0.35	0.03	0.05
Murninnie	0.52	0.42	0.44	0.39
Mitchellville	0.5	0.50	1	1
Mitchellville	0.75	0.59	0.67	0.76
Pt Pirie	0.67	0.69	0.20	0.38
Murninnie	0.5	0.49	0.10	-
Weighted mean	0.49	0.49	0.33	0.55

5.3.3.2 Batch fecundity

The number of fish which had a batch of hydrated oocytes ready for ovulation was small (n = 31) and so the samples were pooled for the four sampling months. There was wide variation in estimates of batch fecundity for each size group of fish (Fig. 5.15). The linear regression was batch fecundity, $F = 21{,}992 + 36{,}189^{*}$ weight (kg) ($r^2 = 0.50$).

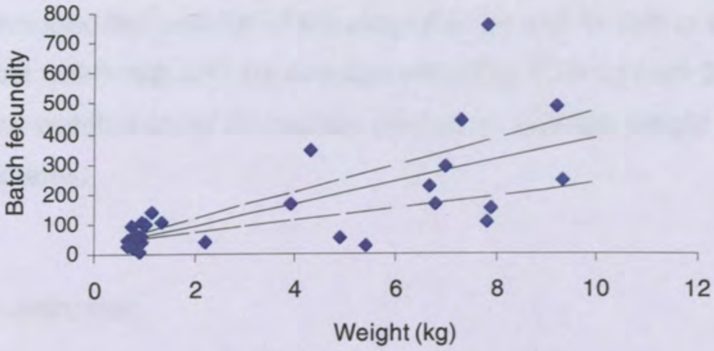


Fig. 5.15 Batch fecundity (oocytes x 1,000) of snapper captured during the spawning seasons of 1994 and 1995 in northern Spencer Gulf. The solid line shows the least squares linear regression and the dashed lines show the bootstrapped 95% CIs.

The use of a pooled estimate of batch fecundity assumes that the relationship is similar between months within a year and between years but there were insufficient data in this study to test that assumption.

5.3.3.3 Length-weight relationship and mean female weight

A total of 529 fish were measured and weighed during the DEPM surveys. The non-linear regression established a relationship of whole weight (kg) = 5.958×10^{-5} * LCF (cm) $^{2.692}$ (Fig. 5.16). Comparison of separate male and female length weight relationships showed no significant difference in the slopes of linear regressions of the log-transformed data (analysis of covariance; $P > 0.05$).

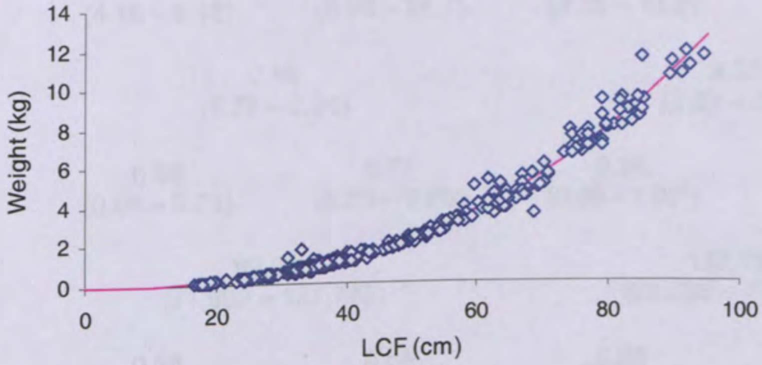


Fig. 5.16 Length weight relationship for northern Spencer Gulf snapper (sexes combined).

The average weight of mature females was estimated to be 2.15 kg for the 1994 samples. This included the addition of the simulated 2+ and 3+ fish to the market measuring sample which reduced the average weight by 0.26 kg from 2.41 kg. The growth of this size distribution for 12 months yielded an average weight of 3.20 kg for the 1995/96 estimates.

5.3.3.4 Biomass estimates

A summary of the parameter estimates used in calculating biomass is shown in Table 5.4.

Table 5.4 DEPM parameter estimates for northern Spencer Gulf. P = egg production, Z = egg mortality, A = spawning area, W = mean weight of mature female, S = proportion of females spawning by weight, F = batch fecundity of average weight female, R = sex ratio by weight, B = spawning biomass. The numbers in parentheses indicate bootstrap 95% CI.

	November 1994	December 1994	December 1995	January 1996
P (eggs.m^{-2}.day^{-1})	1.19 (0.84 – 1.65)	4.68 (1.80 – 4.83)	4.17 (2.16 – 7.44)	-
Z (day^{-1})	0.66 (0.38 – 0.70)	0.21 (0.10 – 0.45)	0.55 (0.0 – 1.32)	-
A (km^2)	4,948	5,542	1,968	
P x A (x 10^9 eggs.day^{-1})	5.90 (4.16 – 8.18)	25.9 (9.96 – 26.7)	8.21 (4.25 – 14.6)	-
W (kg)	2.15 (1.78 – 2.56)		3.20 (2.80 – 3.78)	
S	0.58 (0.06 – 0.73)	0.77 (0.66 – 0.98)	0.96 (0.68 - 1.00[1])	
F (eggs.day^{-1})	99,798 (71,602 – 127,773)		137,797 (99,232 – 192,557)	
R	0.58 (0.37 – 0.74)	0.55 (0.48 – 0.73)	0.66 (0.28 – 1.00)	
B (tonnes)	378 (222 – 2,880)	1,318 (448 – 1,549)	302 (134 – 915)	-

Biomass was estimated at 378 tonnes for the entire study area in November 1994. The poor precision for this estimate was driven by large variation in the proportion of females spawning between samples, that ranged from 0.06 to 0.73 (Table 5.4). The area for the analysis of this survey was not stratified *post hoc* to a main spawning area but demonstrated the advantages of doing so when adequate adult samples allow. The estimates of biomass for December 1994 and 1995 were calculated only for the main spawning area identified by egg distributions (delineated in Fig. 5.11b, c). There were inadequate adult samples for *post hoc* stratification. No biomass estimate was made for January 1996 as egg mortality (and therefore egg production) could not be calculated.

5.4 Discussion

At the time of sampling, this study was the first use of the DEPM on *P. auratus* in a small scale fishery and only the second application to this species overall. It has provided valuable information on the life history of the species in northern Spencer Gulf, including indications of areas of spawning concentrations obtained from both egg distributions and spatial variation of spawning frequencies. Importantly, it has also highlighted some of the sampling difficulties associated with the use of DEPM in a fishery of this size, and can provide guidance for the design of future studies of this type.

5.4.1 Spawning patterns

The study was the first to quantitatively sample snapper eggs in South Australia and provided the first detailed spatial information on spawning patterns in northern Spencer Gulf. Eggs were recorded from most sampling stations on at least one cruise but their densities were consistently higher in the central part of the study area. This pattern was supported by the proportion of females in spawning condition that ranged from 0.69 to 1.0 in the central region compared to 0.0 to 0.25 in samples captured in areas to the north. There was at least some evidence that more spawning occurred in the western part of the Gulf (within the central region), with generally higher egg densities and spawning proportions. However, more detailed sampling would be needed to further define these areas.

P. auratus were found in spawning condition in each of the four sampling months indicating that the spawning season extends at least from mid-November to mid-January in northern Spencer Gulf. Egg densities in the central region were higher in December 1994 and 1995 than in November 1994 or January 1996 suggesting a peak sampling time but, again, more detailed temporal sampling would be required to confirm such a peak. These findings are generally consistent with other studies of the spawning seasons of temperate latitude snapper stocks of Australia and New Zealand (Crossland 1977b; Lenanton 1974; MacDonald 1982; Zeldis 1993). By comparison, other Australian stocks with distributions between latitudes approximately 21^{0}S to 27^{0}S have been reported to spawn between June and September (Ferrell and Sumpton 1997; Jackson and Cheng 2001), and *P. major* from late March to early June in Japanese and Taiwanese waters (Foscarini 1988; Matsuyama et al. 1988; Tanaka 1980).

5.4.2 Spawning biomass estimation

This study provided the first direct estimates of snapper biomass in any South Australian waters. The absence of adequate adult samples from the area outside of the main spawning area precluded a precise assessment of the whole stock in the study area. Where this was attempted (in November 1994), the spatial variation in both egg densities and spawning proportion yielded an estimate with bootstrap 95% confidence intervals approaching one order of magnitude. The coefficient of variation of the remaining estimates was in the order of 66 – 200%, which compares favourably with other studies of *P. auratus* (Jackson and Cheng 2001; Zeldis and Francis 1998).

The low level of precision of DEPM biomass estimates has been a common problem in many studies and has generally been attributed to the poor precision of estimates of egg mortality (Z), which is necessary to estimate egg production P_0 (Alheit 1993). Recent snapper studies in Shark Bay, Western Australia have used adaptive sampling to improve this precision, and this shows some promise where spawning patterns are unknown and/or variable (Jackson and Cheng 2001). The present study was limited both in sampling effort and a lack of knowledge of spawning patterns prior to sampling. The results suggest that a stratified sampling approach, using the central region as the primary stratum, would improve precision. Stratification would also assist the precision of the spawning proportion that showed lack of spatial synchrony throughout the study area.

The DEPM study was conducted at a time of near record low commercial catches and so it was expected that biomass would be relatively low. The November 1994 estimate of 1,318 tonnes represented approximately 5.6 times the combined annual commercial / recreational catch of 234.3 tonnes in 1995/6 for the study area (McGlennon and Kinloch 1997). This represents an exploitation rate of 17.8%.

The DEPM study was a valuable attempt to gain a direct estimate of biomass for this heavily fished species in northern Spencer Gulf. The estimates suggest that future attempts would be more effective (better precision, better spatial representation) if:

1) the study is conducted in times of high biomass (i.e. when catches are high) to increase the numbers of adult samples and
2) by stratifying the study area and sampling for eggs more intensively in the central region.

A further attempt was made to use DEPM to estimate spawning biomass in northern Spencer Gulf in 2000 (Fowler 2002). Although the station with the highest abundance of eggs was the same as reported in this study (adjacent to Franklin Harbor near Cowell), he found little other similarity in egg distribution between 1994 and 2000. The latter study failed to produce a biomass estimate due to an inability to estimate Z and P_0 meaningfully from the samples of eggs collected.

The primary purpose for conducting the DEPM was to provide an independent estimate of biomass to scale the biomass projections in the population model (Chapter 8). Despite the sampling difficulties encountered, the December 1994 survey yielded an intuitively reasonable estimate of biomass, based on the resulting exploitation rate and comparison to snapper biomass estimates in other fisheries, and is used as one of the data to which the model is fitted.

Chapter 6. Residency and migration rates of *Pagrus auratus* in Spencer Gulf.

6.1 Introduction

Snapper (*Pagrus auratus)* populations throughout the western Pacific are considered to be a single species with a number of independent and reproductively isolated populations distributed throughout a discontinuous range (Paulin 1990). The species has a continuous distribution across southern Australia but genetic studies of fish from Victoria and South Australia have found evidence of population sub-structuring between fish found north of the Murray Mouth and those found further to the south and east (MacDonald 1980; Donnellan and McGlennon 1996). However, no evidence of sub-structure has been found amongst populations from the main South Australian fishing areas of the Gulfs and adjacent shelf waters (Donnellan and McGlennon 1996). Consequently, the fishery is managed as a single stock (Jones et al. 1990; McGlennon and Jones 1997). The northern Spencer Gulf (NSG) snapper population, which is the focus of this study, is therefore part of a larger South Australian population (Donnellan and McGlennon 1996). To model the dynamics of the NSG population, as well as to better manage this major fishing area, a knowledge of the movement patterns and interaction with snapper in southern Spencer Gulf (SSG) and shelf waters is needed.

A general life history model for snapper in Australia and New Zealand has been developed based on the results of tagging studies, fishery catch statistics, fishers' observations and field observations of the distribution and abundance of different size and age classes. This model involves both a "resident" and "migratory" component to the population. Tagging studies have consistently shown a relatively high proportion of recaptures close to their point of release even after significant time at liberty (Paul 1967; Crossland 1976; Jones 1984a). Yet other recaptures in these studies demonstrated the capacity of snapper to travel considerable distances. Trawl surveys and diver observations of fish generally < 4+ age have shown seasonal and age related changes in abundance and distribution (Paul 1976; Kingett and Choat 1981; Horn 1986; Francis 1995), with dispersal from inshore shallow waters increasing with age occurring during the colder months. Mature fish then aggregate at spawning grounds during spring and early summer, where they are targeted by fishers.

The tagging data showing little movement of most snapper together with catch statistics recording snapper catches throughout the year, has led to the belief that a proportion of the snapper population remains "resident" throughout the year. On the other hand, strong seasonal changes in catches, the observed seasonal changes in abundance, and tag recaptures that show significant movement have contributed to an additional "migratory" component of the population. The migration pattern is generally considered to involve a seasonal inshore-offshore movement, with dispersal onto feeding grounds after spawning, wider dispersal into deeper water during winter and then a return to inshore spawning grounds in spring (Annala et al. 2000). Fishers have long considered that resident and migratory (or schooling) snapper can be discriminated by physical differences (eg. colour, size of hump on the forehead, and degree of fat). The morphometric analyses of fish in Shark Bay support those conclusions (Moran et al. 1998).

The concepts of both residency and annual spawning migrations have also been reported in South Australia (Jones 1981; Jones 1984a; McGlennon and Jones 1997). Movement of snapper in and out of NSG was first demonstrated by tagging studies conducted from 1977 to 1980 as described by (Jones 1981). These studies showed that fish tagged in NSG were either recaptured at or near their release site or had travelled significant distances into SSG. He concluded that the longer movements were made by small snapper (< 4 years old) which schooled on reefs during spring and summer but which dispersed into deeper water and onto the shelf during winter. He also concluded that older fish (> 12 years) returned to shallow NSG waters but remained thereafter. The tagging results also showed some exchange of fish between Spencer Gulf and adjacent shelf waters, with one fish moving from Investigator Strait to NSG and one from SSG moving onto the shelf south of Eyre Peninsula.

The possibility of a resident population supplemented by an annual influx of migratory fish from the shelf has important implications for fisheries management. In particular, the proportion of the population which is resident in highly fished waters as opposed to those which seasonally migrate to lightly fished offshore waters must influence the appropriate management strategy. Previous studies have not attempted to quantify these proportions or rates of movement between regions. Data collected from a tagging study carried out in South Australian waters from 1987 to 1992, together with the use of a spatial movement model, offered the opportunity to do so. The tagging study was initiated in 1987 by David Hall, Research Officer of the then Department of

Fisheries, and later became the responsibility of the author in 1990 when Mr Hall left the Department. The analysis described in this Chapter:

1) provides an overview of the results of the tagging study as it relates to NSG;
2) uses a movement model to estimate residency and annual movement rates between NSG, SSG and shelf waters, including size related differences in those parameters, and;
3) investigates the seasonality of those movements into and out of NSG.

6.2 Methods

This section first provides a general description of the tagging programme and is then followed by the methods of analysis used to quantify rates of movement.

6.2.1 Overview of the tagging programme

Tagging was done as a cooperative programme with the voluntary participation of recreational and commercial fishers, as well as Departmental research staff. Two types of tags were used: Hallprint loop tags (models SLA and SLB) and Hallprint dart tags (models PDS and PDA) (Fig. 6.1). Two different sizes of each tag-type were used according to the size of the fish. Loop tags were inserted dorsally in a position anterior to the dorsal fin and dart tags were inserted through the dorsal fin pterygiphores near the anterior of the fin (Fig. 6.2).

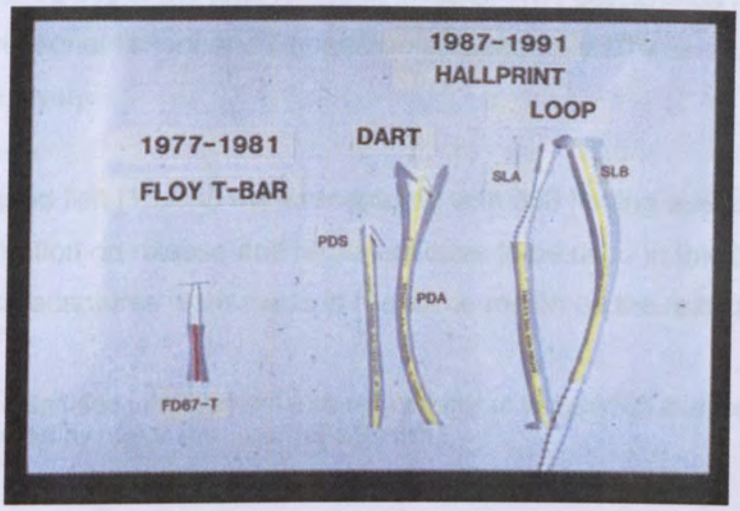


Fig. 6.1 Hallprint tag types used in South Australian snapper tagging programmes. The T-bar tag on the left was used in studies described by Jones (1981) and the dart and loop tags were used in the study described in this Chapter.

Fig. 6.2 Location of the insertion points of loop and dart tags.

A total of 4,143 *P.* auratus were tagged and released in South Australian waters from 1987 to 1992, with recaptures continuing until 1996 (Table 6.1). The intent of the tagging programme was to provide as much geographic coverage as possible by involving fishers from many areas of the State. However, snapper are most readily caught in Spencer Gulf which is where recreational and commercial fishers naturally focus their efforts. Therefore, the majority (91.6%) of tagged snapper were released in

Spencer Gulf, with 72.7% of the total released in NSG. The percentage released by commercial, recreational fishers and Departmental research staff was 16.6%, 33.6% and 49.8% respectively.

A total of 646 tagged fish (15.6%) were recaptured with 568 having adequate geographic information on release and recapture sites to be used in this analysis (Table 6.1). Most recaptures were made in the same region as the release.

Table 6.1 Tagging data used in movement models: number of tagged fish that were released and recaptured by region and year (all size fish).

	Year										
	87 [1]	88	89	90	91	92	93	94	95	96	
Tag releases											Total
Region											
NSG	222	928	904	507	456	51	0	0	0	0	3068
SSG	0	58	289	184	213	62	0	0	0	0	806
Shelf	5	84	51	60	69	0	0	0	0	0	269
											4,143
Tag recaptures											
Released in NSG											
NSG	5	50	102	89	55	81	19	7	1	1	410
SSG	0	2	1	2	3	0	2	0	0	0	10
Shelf	0	0	0	0	0	0	0	0	0	0	0
Released in SSG											
NSG	0	0	0	5	3	1	2	1	0	0	12
SSG	0	2	17	26	13	25	14	1	0	0	98
Shelf	0	0	0	0	0	2	0	0	0	0	2
Released in Shelf											
NSG	0	0	0	0	0	0	2	0	0	0	2
SSG	0	0	0	0	0	0	0	0	0	0	0
Shelf	0	3	10	3	4	4	8	1	1	0	34
											568

Most fish released in all regions except West Coast waters were less than the minimum legal length of 38 cm total length (or approx 33 cm caudal fork length (LCF)) (Fig. 6.3). This reflected not only a relative abundance of smaller fish during the tagging programme but also a greater willingness of fishers to release undersize fish than

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[1] Period Oct- Dec only

those above the legal minimum length. The relatively small number (n = 37) of snapper released in West Coast waters showed a very different length distribution with most in the 50 – 60 cm LCF range, which was lacking in Gulf releases. The length of recaptured fish showed a similar distribution to releases after allowing for growth during time at liberty.

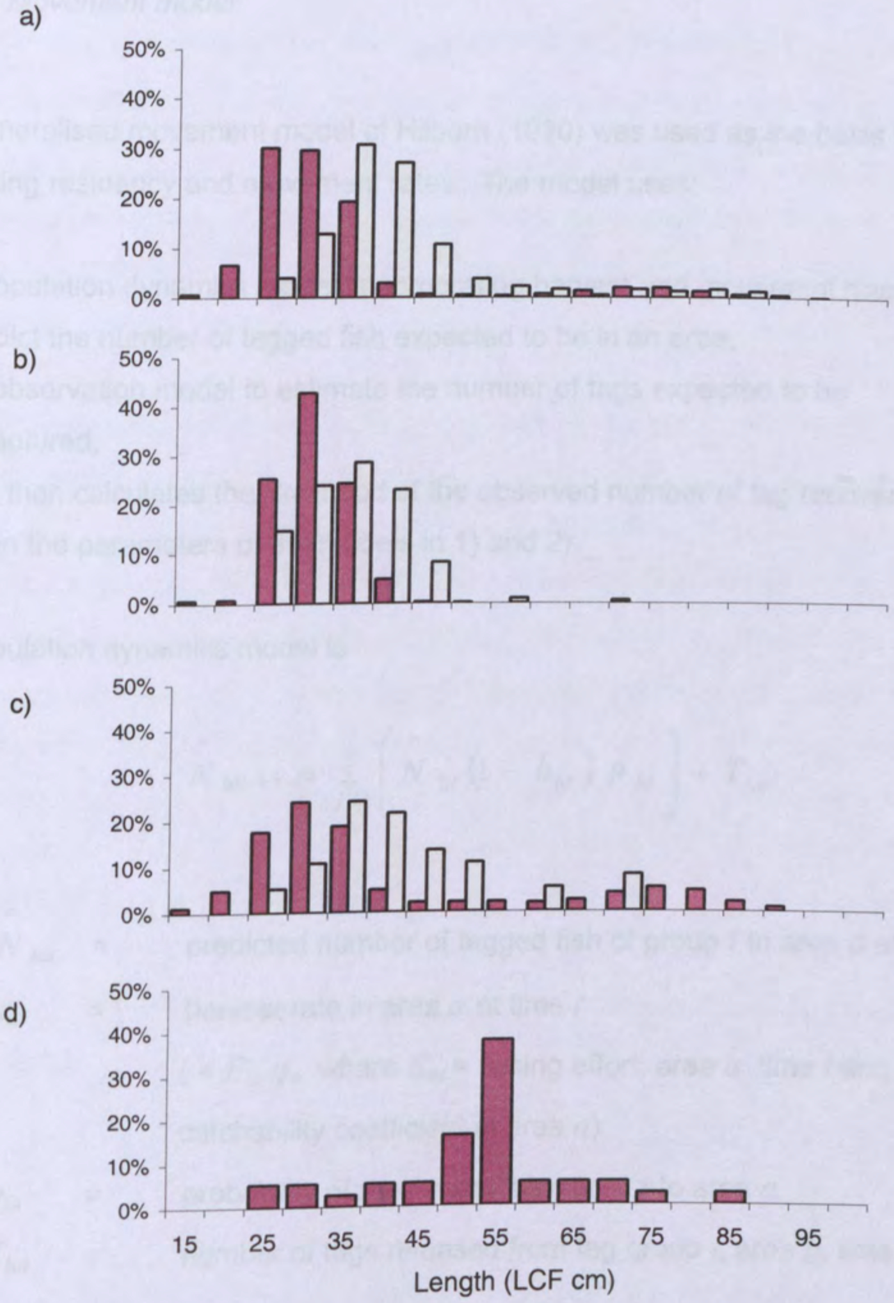

Fig. 6.3 Length frequency distributions for releases (red) and recaptures (yellow) in a) NSG, b) SSG, c) Gulf St Vincent & Investigator Strait and d) West Coast waters. The 3 West Coast recaptures were 280, 514 and 556 mm LCF respectively.

6.2.2 Estimation of residency and movement rates

6.2.2.1 Movement model

The generalised movement model of Hilborn (1990) was used as the basis for estimating residency and movement rates. The model uses:

1) a population dynamics model, incorporating harvest and movement rates, to predict the number of tagged fish expected to be in an area,
2) an observation model to estimate the number of tags expected to be recaptured,
3) and then calculates the likelihood of the observed number of tag recoveries given the parameters of the models in 1) and 2).

The population dynamics model is

$$\hat{N}_{iat+1} = \sum_{j=1}^{n} \left(\hat{N}_{ijt} \left(1 - h_{at}\right) p_{ja} \right) + T_{iat} \qquad \text{(Eq. 6.1)}$$

where

$\hat{N}_{iat}$ = predicted number of tagged fish of group i in area a at time t

h_{at} = harvest rate in area a at time t (= $E_{at}\, q_a$ where E_{at} = fishing effort, area a, time t and q_a = catchability coefficient in area a)

p_{ja} = probability of movement from area j to area a

T_{iat} = number of tags released from tag group i, area a, time t

For the base model, and other models unless otherwise specified;

- the tag group included all sizes of snapper,

- the areas were Northern Spencer Gulf (NSG), Southern Spencer Gulf (SSG) and Other (O) shelf waters (ie. Investigator Strait and West Coast waters) [2],
- and time strata were years.

The population dynamics model estimates movement probabilities (p_{ja}) and the catchability coefficient (q_a) for each spatial stratum, and requires inputs of the number of tag releases (T_{iat}) and fishing effort (E_{at}) for each spatial and time stratum. Data on tag releases were available directly from the tagging database (Table 6.1), with date and location of releases recorded by the taggers and later coded for latitude, longitude and statistical fishing blocks.

Calculation of fishing effort was more problematic as the suite of geartypes targeting snapper included commercial handlining and longlining as well as recreational handlining. In addition, some regions had small amounts of other commercial effort such as fish traps and nets. The model could potentially accommodate segregated effort by estimating gear specific values of q_a, but the parameters would be confounded with each other. It was decided therefore, to calculate a single standardised effort by using the ratio of relative catch per unit of targeted effort (CPUE) for each method. The CPUE (kg.boatday^{-1}) of commercial handlining (HL) was used as the denominator of the standardisation ratio as it was the dominant fishing method in all areas (Table 6.2).

Standardised fishing effort (StFE) (boatdays) for each region R in year t was determined by

$$StFE_{Rt} = \sum_{i=1}^{n} FE_{it}\left(\frac{CPUE_{it}}{CPUE_{HLt}}\right) \qquad \text{(Eq. 6.2)}$$

where FE_{it} = fishing effort (boatdays) for method i in year t

$CPUE_{it}$ = catch per unit effort (kg.boatday^{-1}), method i, year t

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[2] NSG comprises Blocks 11, 19, 20, 21, 22, 23; SSG comprises Blocks 29, 30, 31 32, 33; Shelf (O) comprises Blocks 8, 9, 10, 14, 15, 39, 40, 42, 44 (see Fig. 2.3 in Chapter 2)

Table 6.2 Raw and standardised annual fishing effort (targeting snapper) for the three regions for the period 1987 – 1996. HL = handline, LL = longline, HN = haul net, Other = miscellaneous commercial methods, REC = recreational handline

	Raw & standardised (parentheses) targeted effort by method (boatdays)					Total standardised effort
	HL	LL	HN	Other	REC	(boatdays)
Northern Spencer Gulf						
1987[3]	595	184 (131)	3 (13)	0	1,353 (80)	819
1988	1254	1047 (443)	74 (404)	0	5,412 (319)	2420
1989	1746	948 (635)	36 (391)	0		3091
1990	1563	823 (376)	45 (321)	0		2579
1991	1866	933 (483)	13 (70)	0		2738
1992	1880	933 (733)	76 (266)	0		3198
1993	1637	1220 (931)	29 (93)	0		2980
1994	1492	937 (759)	10 (35)	0		2605
1995	1606	950 (823)	2 (2)	0		2750
1996	1490	1133 (850)	1 (4)	0		2663
Southern Spencer Gulf						
1987[3]	320	64 (49)	0	0	558 (22)	391
1988	790	113 (90)	0	0	2238 (87)	967
1989	833	108 (47)	0	0		967
1990	855	86 (38)	0	0		980
1991	838	182 (123)	0	0		1048
1992	729	173 (134)	0	0		950
1993	664	135 (99)	0	0		850
1994	405	76 (83)	0	0		575
1995	446	89 (59)	0	0		592
1996	473	103 (43)	0	0		603
Gulf St Vincent & shelf waters						
1987[3]	613	75 (93)	0	25 (33)	2485 (62)	801
1988	1115	643 (869)	0	79 (194)	9942 (249)	2427
1989	841	573 (532)	0	157 (220)		1842
1990	891	411 (514)	0	108 (56)		1710
1991	662	341 (435)	0	63 (60)		1406
1992	495	344 (598)	0	62 (135)		1477
1993	518	399 (395)	0	65 (85)		1247
1994	380	392 (420)	0	35 (47)		1096
1995	248	226 (342)	0	13 (51)		890
1996	278	182 (162)	0	32 (79)		768

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[3] Oct – Dec only

The commercial snapper fishing effort data for each method, region and month were available from the statistical reporting database. But comparable data were only available for a single year for the recreational fishery that were collected from 1994-96 in the latter stages of the tagging programme (McGlennon and Kinloch 1997). This study reported a recreational creel survey conducted from 1994-6 in all regions of the State, and included targeted fishing effort for snapper (as well as other species). A single year's data (April 1994 – March 1995 for Gulf St Vincent and Kangaroo Island; April 1995 – March 1996 for Spencer Gulf and West Coast) were available for each region. The use of the single year's data for the recreational fishery makes the unlikely assumption that recreational fishing effort was constant over time and space during the 1987 – 96 period. However, the contribution of recreational fishing effort to the total standardised effort in 1996 was relatively low in the main Spencer Gulf regions (12 – 14.4%) but was higher (32.4%) in GSV and shelf waters where commercial effort for this species is low.

Following estimation of the number of tagged fish in each area with the population dynamics model, the observation model was used to predict the number of tag recaptures expected for each area and year. This model again followed Hilborn (1990) and assumes a direct relationship between fishing effort and tag recaptures

$$\hat{R}_{iat} = \hat{N}_{iat}\, q_a\, E_{at} \qquad \text{(Eq. 6.3)}$$

where $\hat{R}_{iat}$ = number of tags recovered from tag group *i*, area *a*, time *t*. The observation model therefore requires no further data input and introduces no further parameters to estimate.

Finally, the movement probabilities p_{ja} and catchability coefficients q_a were estimated by maximising the likelihood of the observed tag recaptures with those predicted by the observation model. The Poisson likelihood function was used (Hilborn 1990), where the total likelihood for all observed recaptures given the parameters of the population dynamics and observation models, is

$$L(R|p,q,E,T) = \prod_{i} \prod_{a} \prod_{t} \frac{e^{-\hat{R}_{iat}}\, \hat{R}_{iat}^{\,R_{iat}}}{R_{iat}!} \qquad \text{(Eq. 6.4)}$$

6.2.2.2 Model fitting and testing

The parameters were estimated by maximising the negative log-likelihood of Eq 6.4 using the Solver function in MS Excel. The negative log-likelihood was required within Solver to reduce the scale between the parameter estimates and the objective function. Five different models were specified, using a combination of two or three spatial regions, by incorporating tag shedding rates and by limiting the dataset to small fish (< 40 cm LCF).

a) The simplest model used fishing effort, tag releases and recaptures in northern (N) and southern (S) Spencer Gulf to estimate residence rates in each region (p_{NN}, p_{SS}) as well as the probability of movement between the two (p_{NS}, p_{SN}).

b) The general movement model can also include other parameters such as tag shedding, tagging mortality and non-reporting of tags (Hilborn 1990). The dart tags used in this study were shown to have high shedding rates (58.6%) for this species in the first year in captivity, whereas loop tags have very low rates (4.3%) (McGlennon and Partington 1997). The rate of tag shedding was not re-estimated as a model parameter as it is highly confounded with fishing and natural mortality and movement (Hilborn 1990). As an alternative, the tag shedding rates from the captivity experiment were coded into the calculations. The rate used was the average tag retention rate (1 – tag shedding) of loop and dart tags in the first year, weighted by the relative proportion of tags released in that year (Table 6.3), and was only applied to the number of tags released in that year, T_{iat}. Tag shedding was low after the first year in captivity (McGlennon and Partington 1997) and was not incorporated in the model. The population dynamics model including tag shedding was therefore

$$\hat{N}_{iat+1} = \sum_{j=1}^{n}\left(\left(\hat{N}_{ijt} * TR_t\right)\left(1 - h_{jt}\right)p_{ja}\right) + T_{iat} \qquad \text{(Eq. 6.5)}$$

where TR_t = average tag retention during first year, where the average is weighted by proportion of loop and dart tags released in year t (Table 6.3).

Table 6.3 Number of dart (D) and loop (L) tags released by region and year, and weighted average tag retention rates (TR).

	NSG			SSG			SHELF		
	D	L	TR	D	L	TR	D	L	TR
1988	751	177	51.78%	5	53	91.03%	60	20	55.00%
1989	77	818	91.04%	0	289	95.71%	0	73	95.71%
1990	40	466	91.42%	5	179	94.24%	0	94	95.71%
1991	136	320	79.52%	41	172	85.26%	10	79	89.61%
1992	0	51	95.71%	0	62	95.71%	0	62	95.71%

The two strata model with tag shedding was calculated using data from all (n = 530) recaptures (Model II) and using data only from fish released and recaptured < 40 cm LCF (n = 491) (Model III). The use of the latter data reflected an interest in potential size-related differences in movement noted in an earlier tagging study (Jones 1984a) and in the recapture data of this study. An alternative approach would have been to treat the two different size groups (< 40, > 40cm) as different tag groups in the model, but only a relatively small number of tags were released (n = 422) and recaptured (n = 39) for fish > 40 cm LCF and only a single fish tagged > 40 cm LCF moved between regions. The former approach of analysing small fish only was therefore preferred.

c) The residual of Models I – III includes an indirect estimate of movement out of Spencer Gulf (along with natural mortality, etc). However, data on tag releases and recaptures outside of the Gulf were available for a more direct estimate, although only 4 recaptures provided evidence of exchange between Spencer Gulf and shelf waters (Table 6.1). Two were recaptured in NSG, with one released in Investigator Strait (Block 44) and the other in West Coast waters (Block 15). The other two were released in southern Spencer Gulf and recaptured in adjacent shelf waters. To incorporate these data, the movement model (including tag shedding) was re-estimated using the additional spatial stratum of "shelf" (O) waters. This included Investigator Strait and all West Coast waters and reflected all areas where there was evidence of exchange with Spencer Gulf. The only area excluded, therefore, was northern Gulf St Vincent. The model was estimated using all recapture data (n = 569) (Model IV) and using data only from fish released and recaptured < 40 cm LCF (n=522) (Model V).

In summary then, the five different models were:

1) base model of annual movement between two spatial strata only (NSG and SSG), all fish sizes included (Model I),
2) Model I plus coded value for tag shedding in year 1 (Model II),
3) Model II with fish < 40 cm LCF only (Model III)
4) Model of annual movement between three spatial strata (NSG, SSG and Shelf), all sizes and tag shedding included (Model IV),
5) Model IV with fish < 40 cm LCF only (Model V)

The sum of residence and movement rates typically do not add to 1, with the residual identifying natural mortality and movement to other areas (Hilborn 1990). In Models I - III, this movement identified emigration from Spencer Gulf and in Models IV and V signified movement outside of the main fishing areas.

Confidence intervals for the movement probabilities and catchability coefficients were estimated using a bootstrap procedure (Manly 1997). The time series 1988 – 1996 was split as two separate periods for the purposes of resampling – the period of tag releases and recaptures (1988 – 1992) and the remaining period (1993 - 96) where no tags were released but recaptures continued. Data for the initial period of October – December 1987 when tagging commenced was not included in the resampling. The data inputs for each year from 1988 – 1992 (fishing effort, tag releases and recaptures) were resampled with replacement to re-populate each of those years. The data inputs for each year from 1993 – 1996 (fishing effort, tag recaptures) were then resampled with replacement to re-populate the remaining years. The movement and catchability parameters were then re-estimated with the resampled time series. This was repeated 100 times and confidence intervals taken as the 0.05 and 0.95 percentiles of the bootstrap distribution.

6.2.2.3 Seasonal north-south movement

The movement model estimated residence and movement rates on an annual time scale. Resident fish, therefore, may include those which may have migrated out of the region and returned. Estimation of these within-year seasonal migrations could be incorporated into the movement model given sufficient data. This should logically include only those fish recaptured within one year of release. However, this limitation reduced the number of tag movements between regions to 7 in this study and, after allocation to annual and seasonal strata, I did not feel this low number warranted movement estimates by modeling. I have therefore taken a more qualitative approach.

The general hypothesis of within-year movement depicts a dispersal into deeper waters in autumn and winter followed by aggregation onto spawning grounds in late spring and summer. In the Spencer Gulf context, this can be described as a northerly movement of fish in spring to spawning grounds in NSG followed by a southerly dispersal to SSG and beyond in autumn. To investigate this, the data on latitude at time of release and recapture were used as a measure of north-south movement for all mature fish that were >23 cm LCF and at liberty for < 1 year (n = 300). The periods of release and recapture were aggregated into spawning (Oct – Jan) and non-spawning months. Net north-south movement was then plotted against time at liberty for fish released in the spawning season and recaptured a) in the spawning and b) non-spawning seasons, and for those released during the non-spawning season and recaptured c) in the spawning season and d) in the non-spawning season.

6.3 Results

6.3.1 General tag recapture results - distance travelled and time at liberty

More than 90% of fish were recaptured within 20 nautical miles (nm) of their point of release, with nearly 50% showing no net movement (Table 6.4). The maximum distance between the release and recapture points was 330 nm. Smaller fish (< 39 cm LCF) showed a greater tendency to travel, with 8% moving more than 20 nm (Table 6.4). In contrast, only two fish greater than 39 cm LCF travelled more than 20 nm, although the number of recaptures in these size classes was relatively small.

Table 6.4 Distance between points of release and recapture by size class of *P.auratus*.

	Distance travelled (nautical miles)				
	0	1-20	21-50	51-100	>100
Release length (cm LCF)					
<30	157	137	19	10	1
30-39	104	85	9	3	0
40-49	9	5	0	0	0
50-59	3	6	0	0	1
60-69	8	3	1	0	0
70+	4	6	0	0	0
Total	285 (49.9%)	242 (42.4%)	29 (5.1%)	13 (2.3%)	2 (0.4%)

The majority of longer movements within Spencer Gulf were in a southerly direction, with fish released in NSG recaptured near both the western and eastern coasts of the Gulf (Fig. 6.4). There were also two long movements into NSG from a) West Coast waters near Ceduna and b) Investigator Strait near Cape Jervis (Fig. 6.4 inset).

The majority of recaptures (62.5%) occurred within the first year with more than 85% recaptured within 2 years (Fig. 6.5). However, more than 80 tagged fish were at liberty for more than two years, with the longest time at liberty being 2,041 days. There was some evidence of annual periodicity to the recaptures with a strong recapture peak at approximately 360 days and a smaller peak around 720 days (Fig. 6.5a). There was no apparent relationship between distance travelled and time at liberty (Fig. 6.5b).

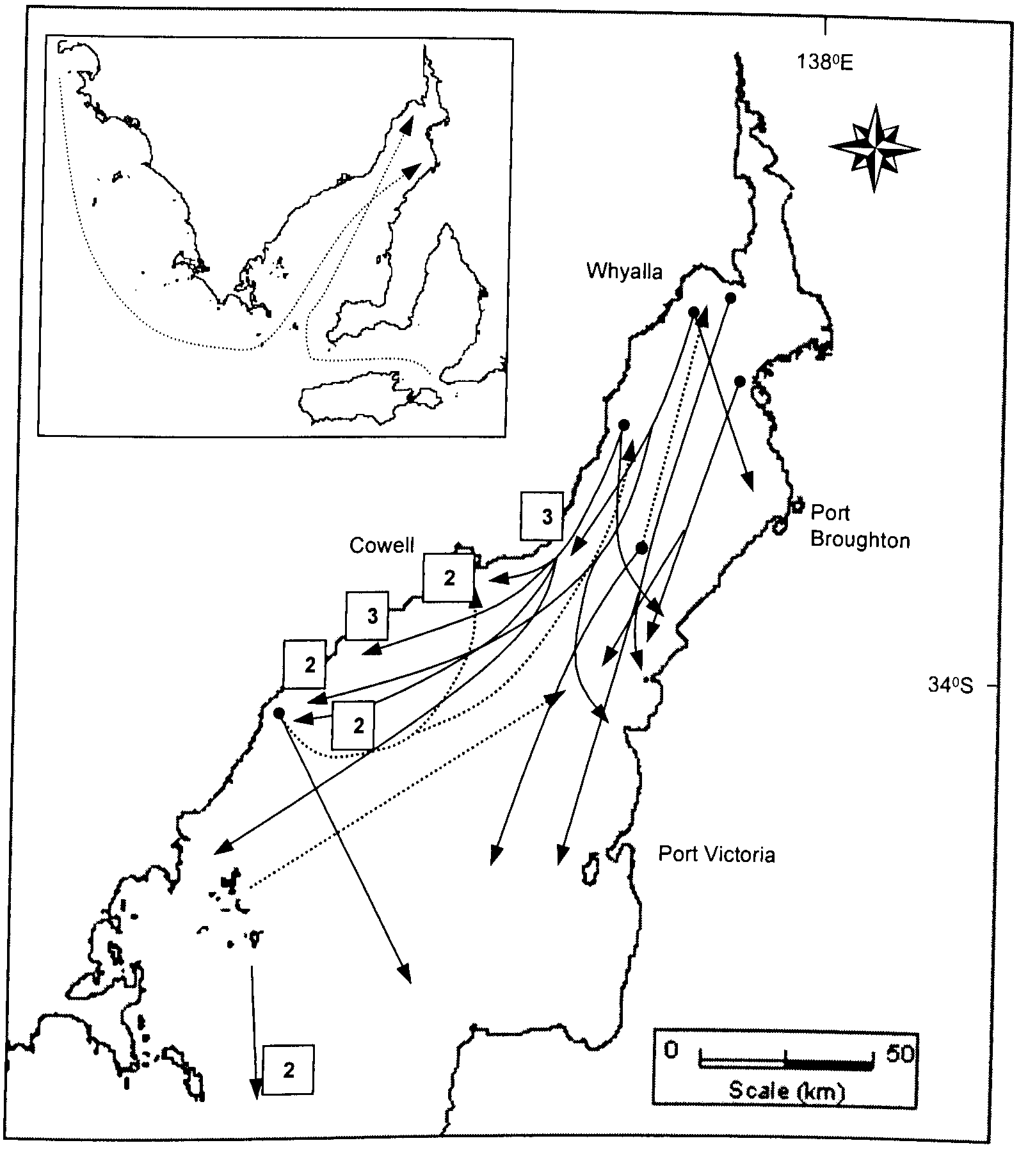


Fig. 6.4 Inferred longer distance (> 30nm) movement of P.auratus in Spencer Gulf 1987 – 1996. Solid lines indicate southerly movement, dotted lines indicate northerly movement, and numbers in text boxes indicate multiple recaptures. Inset: two long distance movements into northern Spencer Gulf.

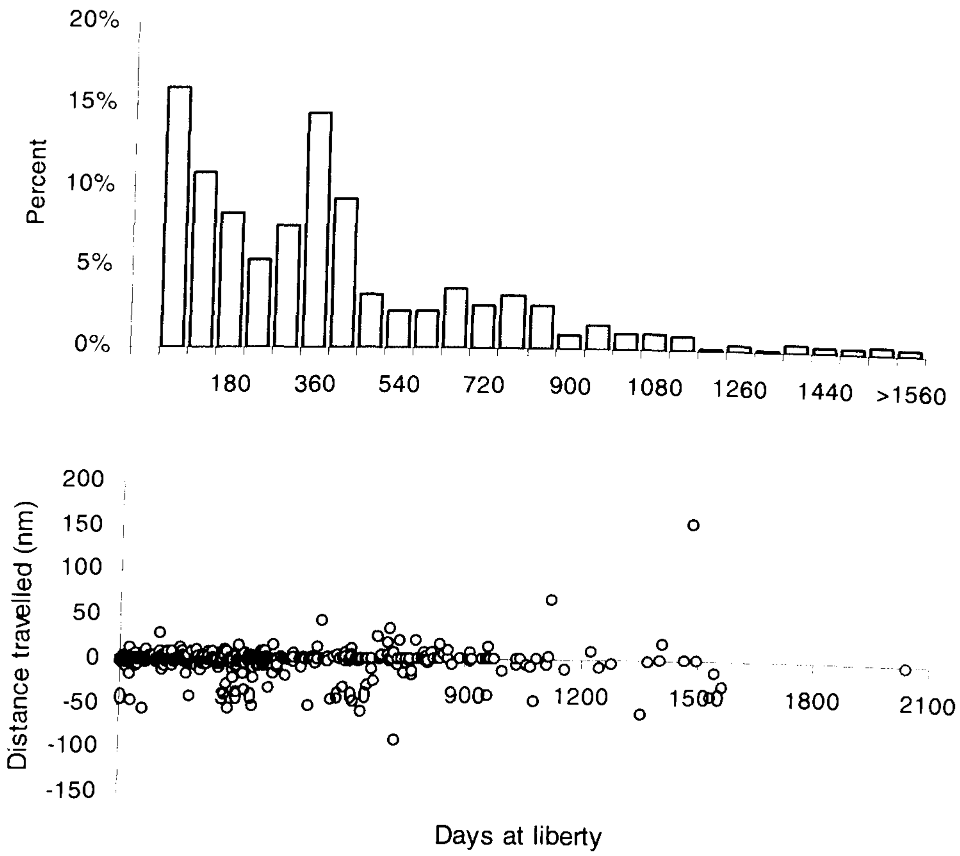


Fig. 6.5 a) Frequency distribution of days at liberty of recaptured snapper in South Australian waters 1987 to 1996; b) relationship between days at liberty and distance between points of release and recapture (+ve = north, -ve = south).

6.3.2 Movement rates

The fit of the simplest model using only tag release and recapture data from northern and southern Spencer Gulf (Model I) was improved by the addition of coded tag shedding rates (Model II) (Table 6.5). Models II - V yielded very similar estimates of movement probabilities and catchability (Table 6.5). The estimated residency rate was approximately 0.58 for NSG and 0.62 for SSG. The probabilities of movement between the regions were estimated at just over 0.02 for p_{NS} and ≈ 0.05 for south – north movement p_{SN}. These estimates changed little when the dataset was restricted to fish < 40 cm LCF (Model III; Table 6.5).

Table 6.5 Estimates of residency and movement rates between northern and southern Spencer Gulf and Shelf waters, and catchability coefficients for each region. The residual is calculated as 1 minus the other probabilities. See text for Model details.

		Probability of movement to			
		NSG	SSG	Shelf	Residual
	From				
Model I	NSG	0.5769	0.0204		0.4027
	SSG	0.0324	0.6709		0.2968
	q	0.000041	0.000074		
- Ln Likelihood		91.87			
Model II	NSG	0.5832	0.0219		0.3949
	SSG	0.0482	0.6222		0.3295
	q	0.000052	0.000101		
- Ln Likelihood		85.97			
Model III	NSG	0.5946	0.0234		0.3819
	SSG	0.0508	0.6224		0.3267
	q	0.000051	0.000103		
- Ln Likelihood		86.77			
Model IV	NSG	0.5914	0.0199	0.0000	0.3887
	SSG	0.0499	0.6351	0.0037	0.3113
	Shelf	0.0403	0.0000	0.7250	0.2348
	q	0.000050	0.000108	0.000058	
-Ln Likelihood		120.73			
Model V	NSG	0.5946	0.0211	0.0000	0.384
	SSG	0.0509	0.6296	0.0177	0.302
	Shelf	0.0121	0.0000	0.8160	0.172
	q	0.000051	0.000114	0.000045	
-Ln Likelihood		111.64			

Further, there was little change to estimates of probability for NSG and SSG when the additional data available from tag releases and recaptures from outside Spencer Gulf were added (Models IV and V) (Table 6.5). However, in contrast to the Spencer Gulf Models (II – III), the restriction of the dataset to fish < 40 cm LCF showed a marked improvement in likelihood. The residency rate for waters outside of Spencer Gulf was estimated at 0.725 for all fish sizes but rose to >0.80 for fish < 40 cm LCF. There were no tag movements from NSG to the Shelf or from the Shelf to SSG but movements in the opposite directions were estimated at approximately 0.01-0.02. These results show an anomaly in the recapture data, with movements from the Shelf to NSG clearly having to pass through SSG but, without recaptures in the database to trigger estimation of that movement, the probability is estimated at 0.

The catchability coefficient estimates were consistent between Models II to V and decreased from NSG to SSG to Shelf waters (Table 6.5). For the period of these data, q estimates yield fishing mortalities ($F = q_a * E_a$) of 0.12 – 0.16 for NSG, 0.06 – 0.11 for SSG and 0.04 – 0.11 for Shelf waters. The residuals (reflecting natural mortality and movement to other areas) were consistently 40% and 32% for NSG and SSG respectively in the two space Models. Natural mortality rates of 10 – 24% have previously been used for *P. auratus* in South Australia (Jones et al. 1990; Annala et al. 2000; McGarvey and Jones 2000), leaving potentially significant movement of 8 – 30% beyond Spencer Gulf to shelf waters. It may therefore have been expected that the residuals would have decreased with the addition of the Shelf water data when explicit movement probabilities were calculated for exchange between Spencer Gulf and the Shelf. However, this did not occur. This may be due to the very low number of recaptures showing exchange between the Shelf and Spencer Gulf (and hence low values of p calculated), but also reflects the large areas of shelf waters which are subject to little fishing pressure and which therefore still represent emigration from the regions covered in this analysis.

The bootstrap resampling used to estimate confidence intervals was limited to Model III (Table 6.6). Mean bootstrap estimates closely followed the model estimates (Table 6.5). The residency rates for NSG and SSG were estimated with relatively low coefficients of variation (cv) of < 30%. The estimates of movement between regions, the residuals and catchability coefficients were estimated with higher cvs.

Table 6.6 Parameter estimates resulting from 100 bootstrap re-samples using Model III.

Parameter	Mean	0.05	0.95	cv
qNSG	0.00007	0.00004	0.00013	42.8%
qSSG	0.00015	0.00004	0.00043	93.2%
pNN	0.47672	0.27075	0.63794	22.8%
pNS	0.02726	0.00517	0.05710	65.2%
Residual NSG	0.49602	0.34320	0.71041	23.3%
pSS	0.59781	0.26580	0.79784	30.4%
pSN	0.03760	0.01075	0.07090	47.5%
Residual SSG	0.36460	0.13433	0.69767	50.9%

The estimated number of tag returns shows good agreement with the observed number in most years (Fig. 6.6). The years of greatest disagreement were 1991 when expectations were greater than the number observed and 1992 when the opposite occurred. It is possible that the 1991 difference was the result of an increase in non-reporting as this was the time of the departure of the programme's originating research officer. Publicity for the programme declined at that time but was revived later to ensure reporting of tags which had long periods at liberty.

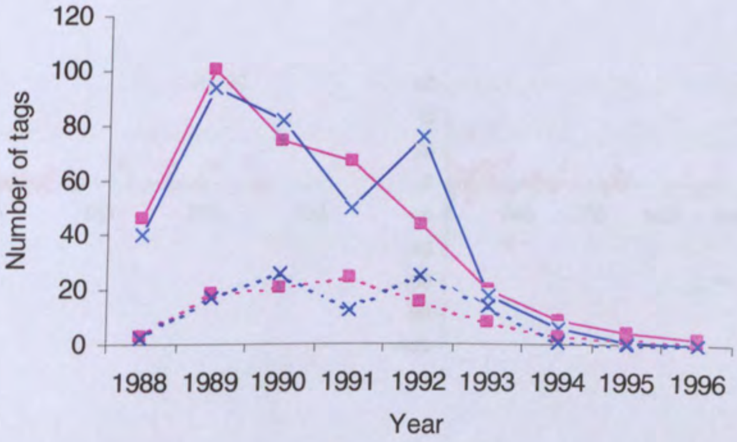
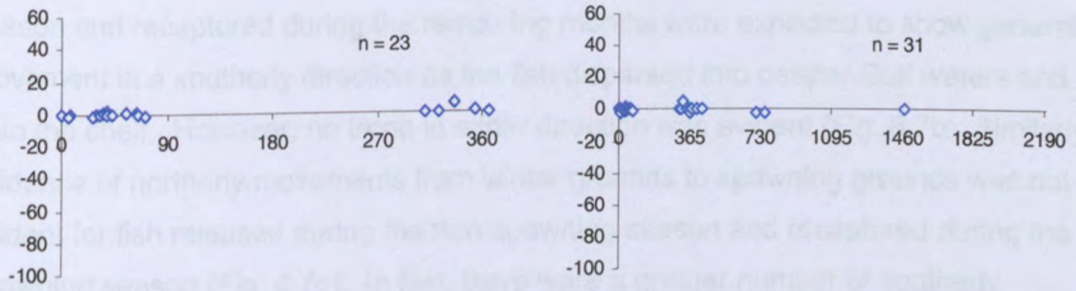


Fig. 6.6 Expected (■) and observed (x) tag returns by year for NSG (solid lines) and SSG (dotted lines) using Model III.

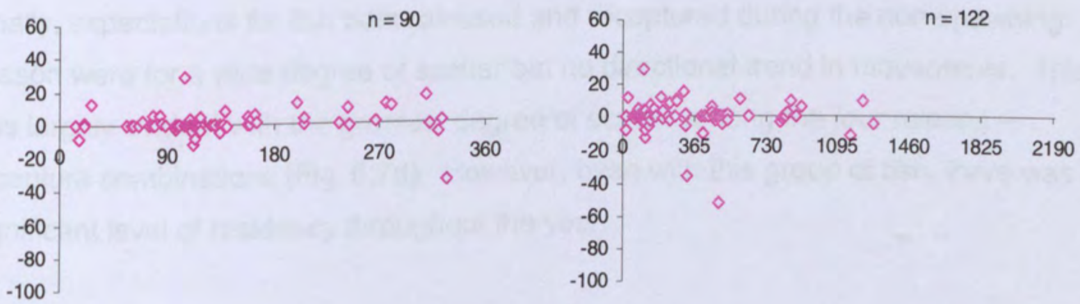
6.3.3 Seasonal movement

The graphs of net north-south movement again show a high level of residency throughout the year irrespective of time of release or recapture (Fig. 6.7). The median distance travelled for all release – recapture combinations was 0.0 nm. Site specificity was particularly evident for snapper released and recaptured during the spawning season (Oct – Jan) (Fig. 6.7a). All fish except 3 were recaptured within 2 nm of their release even up to time at liberty of four years. The remaining three fish were recaptured 5.2 nm from their release site.

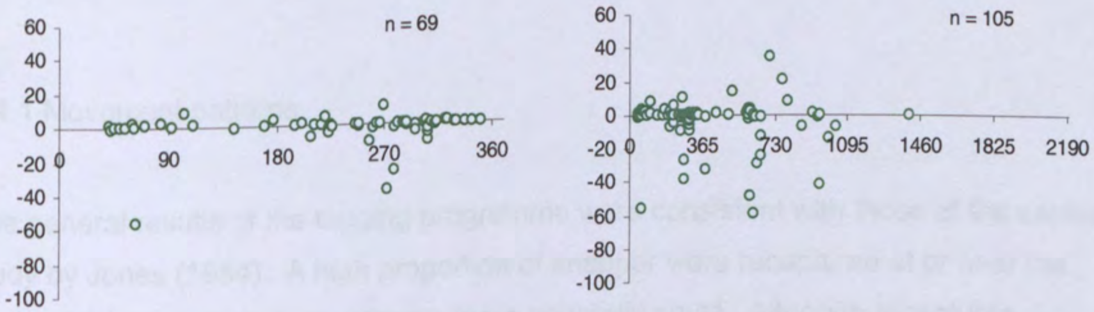
a) Sp – Sp



b) Sp – NonSp



c) NonSp – Sp



d) NonSp – NonSp

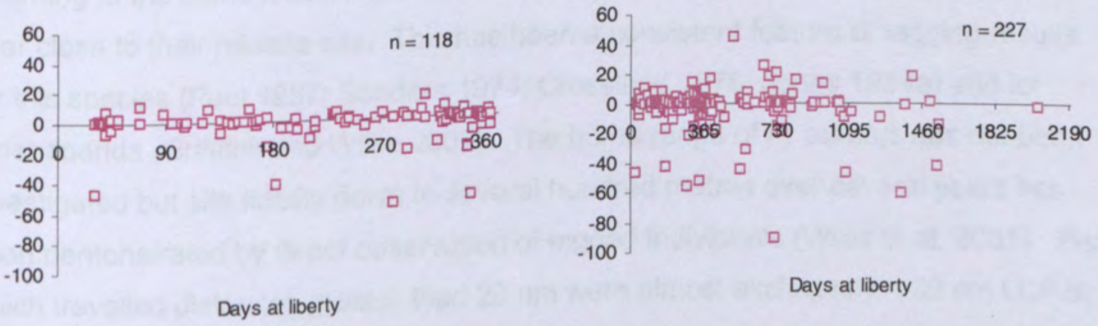


Fig. 6.7 Net north-south movement (nautical miles) for snapper released and recaptured in Spencer Gulf during the spawning (Sp; Oct - Jan) and non-spawning (NonSp) seasons. The graphs in the first column are for time at liberty up to 1 year and in the second column are for all recaptures.

The scatterplots did not show strong evidence of the expected north-south movements between spawning and non-spawning seasons. Fish released during the spawning season and recaptured during the remaining months were expected to show general movement in a southerly direction as the fish dispersed into deeper Gulf waters and onto the shelf. However, no trend in either direction was evident (Fig. 6.7b) Similarly, evidence of northerly movements from winter grounds to spawning grounds was not evident for fish released during the non-spawning season and recaptured during the spawning season (Fig. 6.7c). In fact, there were a greater number of southerly movements observed.

Finally, expectations for fish both released and recaptured during the non-spawning season were for a wide degree of scatter but no directional trend in movements. This was largely evident with the greatest degree of scatter among the four release – recapture combinations (Fig. 6.7d). However, even with this group of fish, there was a significant level of residency throughout the year.

6.4 Discussion

6.4.1 Movement patterns

The general results of the tagging programme were consistent with those of the earlier study by Jones (1984). A high proportion of snapper were recaptured at or near the place of release and net movements were generally small. Although recaptures peaked around annual periods of liberty, suggesting that fish were migrating and then returning to the same locations, there were also many fish captured throughout the year close to their release site. This has been a consistent feature of tagging results for this species (Paul 1967; Sanders 1974; Crossland 1976; Jones 1984a) and for other sparids (Griffiths and Wilke 2002). The home range of *P. auratus* has not been investigated but site fidelity down to several hundred metres over several years has been demonstrated by direct observation of tagged individuals (Willis et al. 2001). Fish which travelled distances greater than 20 nm were almost exclusively < 39 cm LCF at release, which is again consistent with Jones (1984).

It was also of interest that the most significant movements were very similar in both studies (Fig. 6.4): a single fish moved from northern Gulf St Vincent to lower GSV /

Investigator Strait, a single fish moved from Investigator Strait to NSG, one or two fish moved from SSG to the shelf south of Spencer Gulf or Eyre Peninsula. The current study added another dimension with the single tag movement from the West Coast to NSG. Collectively, these recaptures demonstrate some exchange between Spencer Gulf and the shelf between Investigator Strait near Cape Jervis in the east, and offshore from Elliston in the west. In addition, there is evidence of exchange between northern GSV and Investigator Strait from Jones (1984) and this study. Potentially, therefore, exchange could exist between the Gulfs, although no recaptures directly support that.

There was little evidence to support a strong north-south aggregation-dispersal pattern associated with spawning activity. However, movement was more apparent for fish released during the spawning season and recaptured in other months compared to the very high residency or site fidelity evident for releases and recaptures during the spawning season. Dispersal after spawning may therefore be more random than previously thought.

6.4.2 Movement rates

This study provides the first quantitative estimates of movement and residency rates for *P. auratus* in South Australia. Residency estimates of approximately 0.6 for both Spencer Gulf regions have significant implications for management of the fishery in these waters. The estimate of 0.8 is higher for shelf waters but the low numbers and scattered distribution of tag releases in shelf waters mean this estimate must be treated with caution. The concept of residency used in this study is a liberal one, given the large areas of NSG and SSG. Secondly, the arbitrary nature of the division between NSG and SSG is not based on ecological or biological boundaries, but is the division of statistical reporting blocks delimited by degrees of latitude and longitude. However, I believe the concept is adequate for the purpose of management of this species in Spencer Gulf. In essence, the residency rate reflects the proportion of fish which are vulnerable to fishing pressure for all or most of the year, in an area where fishing pressure is greatest for this species.

The concept of a resident and migratory component to the population adds an interesting dimension to the management of the fishery. Emigration from the highly fished Gulf waters provides some relief from fishing mortality for at least part of the year, and maybe for several years for each cohort. This potentially provides a buffer that in turn provides the managers with some comfort that a fish-down of Gulf stocks will be supplemented at some future point by the return of shelf fish. However, this would be a risky strategy until the migration patterns are better understood. It does, however, provide an incentive to monitor fishing of the shelf stocks a little more closely in the meantime.

The estimated rates of exchange between Spencer Gulf and the shelf should be treated with caution. The model estimated low movement rates from southern Spencer Gulf to the shelf of less than 2%, and zero from NSG. However, there is little targeted snapper fishing effort in many areas of the shelf providing little opportunity for tagged fish to be recaptured. This is reflected in the high residuals in these analyses which reflect movement into areas not covered by the analyses. Similarly, the estimated movement rates of < 2% from the shelf to Spencer Gulf are affected by the low numbers and scattered distribution of tag releases in shelf waters.

The movement rates between regions increased slightly when the data were limited to small snapper < 40 cm LCF. The raw movement data from both Jones (1984) and this study suggested that movement rates of small fish are higher than those for larger fish, with very few (if any) large fish moving from NSG. If so, it may have been expected that movement rates would increase (and residency rates decrease) after the data for large fish were excluded from the analysis. Movement from NSG to SSG increased 6-7% in both the 2 and 3 region models, and 5.4% and 2% for movements from SSG to NSG in the 2 and 3 region models respectively. However, the residency rate in NSG also increased for smaller fish and remained virtually unchanged in SSG. The concept of increased mobility of smaller fish is therefore supported by this analysis. There were also no recaptures which offered evidence to refute the concept that larger fish (particularly those over 60 cm LCF) in NSG remain in the region.

6.4.3 Future research

There remain two issues related to the movement of snapper in Spencer Gulf of importance to fisheries management. The more important is the level of mixing between Spencer Gulf and Gulf St Vincent. The dramatic decline of catches in GSV has not reversed even with a cyclical return in Spencer Gulf and it would appear that the two populations are acting independently. Even though the use of passive tags has demonstrated the potential for exchange between the Gulfs, it would appear that any such exchange is extremely limited. Stock discrimination at this spatial scale has been well established in Shark Bay, Western Australia (Johnson et al. 1986; Moran 1987; Edmonds et al. 1989; Edmonds et al. 1999). It is also apparent that passive tags are unlikely to provide further insights into the level of mixing of these stocks. The use of otolith microchemistry would appear to offer the best hope of clarifying and quantifying this issue. Gillanders (2002) has demonstrated the ability of the elemental composition of *P. auratus* otoliths to discriminate between their estuaries of origin and has quantified the level of mixing in the adult populations on that basis. Further, it has been shown that elevated salinities in Shark Bay can be distinguished from ocean waters in the otoliths of *P. auratus* by elevated levels of stable isotopes and strontium/calcium ratios (Edmonds et al. 1999; Bastow et al. 2002). It is therefore possible that the higher salinities of NSG compared to GSV and/or different chemical signatures of the water bodies may afford discrimination of the two stocks via elemental analysis of their otoliths.

The second movement-related issue is the proposal that a proportion of the population migrates to the shelf for a period of years without an annual return to spawn (Jones et al. 1990). This is of relevance to the age-specific fishing mortality for Spencer Gulf fish, and potentially for fisheries management issues of shelf waters. The ability of passive tags to resolve this issue is very limited due to the low fishing pressure in shelf waters. Since it is possible that the lower salinity of shelf waters compared to the salinity of Gulf waters may offer an otolith signature, then otolith microchemistry may also help to resolve this issue (Edmonds et al. 1999). An alternative approach may be the use of archival tags which will became more feasible as they reduce in size and cost (Gillanders et al. 2003).

Chapter 7. Estimation of the growth rate of *Pagrus auratus* in northern Spencer Gulf using age length keys and tag recapture information

7.1 Introduction

Previous estimates of growth rate for South Australian snapper were based on estimates of age using scales and on data derived from tagging programs in the late 1970s and early 1980s (Jones 1984a; Jones 1987). Doubts on the validity of estimates of age from scales for *Pagrus auratus* (Francis et al. 1992) led to the use of otoliths as an ageing medium, and this has in turn resulted in new age length keys (Chapter 3; McGlennon et al. 2000). In addition to these new data, a more recent and comprehensive tagging program (described in Chapter 6) has generated additional data from which growth can be estimated. Thus two new sources of data allowed estimation of snapper growth rates specifically for northern Spencer Gulf, and an opportunity to compare growth rates derived from two independent sources. These newly calculated growth rates will then be used to estimate mean length at age for the age structured population model developed in Chapter 8.

The general aims of this study were to:

1) Estimate growth rates from age length keys based on ages derived from otoliths
2) Estimate growth rates from tag recapture information
3) Compare the growth rate estimates and the merits of the two data sources from these analyses.

Numerous growth models have been used to analyze age length data in fisheries literature, but the most commonly used model is the von Bertalanffy growth curve (von Bertalanffy 1938). Others such as the Richards, Gompertz and logistic curves have also been used and Schnute (1981) provides a useful summary of their formulae. Rather than arbitrarily choose a growth model, Schnute (1981) proposed a generalised four parameter model which incorporates all of the above models and more. The parameter estimates from the general model then lead the investigator to the most appropriate submodel.

Growth parameters using the age length data were estimated as follows:

1) Definition of a separate growth model for otolith samples collected in 1991 and 1994;
2) Comparison of these models with a growth model for the combined samples;
3) Evaluation of the improvement of fit obtained by the addition of seasonal growth terms to the combined data model;
4) Calculation of parameter standard deviations using simulations.

The von Bertalanffy growth curve was also used to estimate growth rates from the tagging data. Francis (1988) indicated that the limitations of the von Bertalanffy parameters with tagging data were due to 1) high correlation between the two parameters L_∞ and K and 2) the inappropriateness of L_∞. To address these limitations, (Francis 1988) re-parameterised the function, added parameters for growth variability, outlier contamination and measurement error, and formulated an analysis program know as GROTAG. An advantage of this program is the ability to estimate parameters separately (but concurrently) for subsets of the data, allowing an evaluation of differences in key parameters between subsets while maintaining common estimates for other parameters. The tagging programme had used two types of tags – dart and loop tags and tag return rates were different for the two (see Chapter 6 for details). It was of interest therefore, whether there was any discernible difference in growth rates from fish tagged with the two tagtypes. Growth rates were estimated from the tagging data using the following steps:

1) Estimation of growth parameters using the combined tagtype data
2) Sequentially adding the seasonality, growth variability, outlier contamination and measurement error parameters and evaluating improvement in model fit
3) Using the "best fit" model for the combined data and re-estimating growth rates for fish tagged with each tagtype separately.

Finally, the different growth rates estimated from the age length data and tagging data were compared. However, since growth rates calculated from these two data sources describe growth in two different ways, they are not directly comparable (Francis 1988). For a standard time interval of (say) one year, the former describes the mean annual growth of fish from age t_1, while the latter describes mean annual growth from length l_1 (independent of age). Although each set of growth estimates could be treated separately, our understanding of growth (and the relative benefits of the data sources) would be greatly enhanced by the ability to compare the respective results. To enable this comparison, the growth estimates derived from the age length keys were converted to the same base (i.e. length) as the rates from the tagging data.

7.2 Methods

The analyses of growth rates are described separately for those derived from age length keys and tag recapture information.

7.2.1 Age length analysis

The sampling and ageing of snapper otoliths were previously described in Chapter 3. The estimates of age derived from otoliths and the lengths (caudal fork length, LCF) of fish from that study provided the data for estimating growth rates. Data from 356 and 455 snapper collected in 1991 and 1994 respectively were used in this analysis (Fig. 7.1). The fish were aged from 2 to 30 and 2 to 34 years in 1991 and 1994 respectively. For this analysis, ages were calculated as decimal years ((date of capture – January 1)/365).

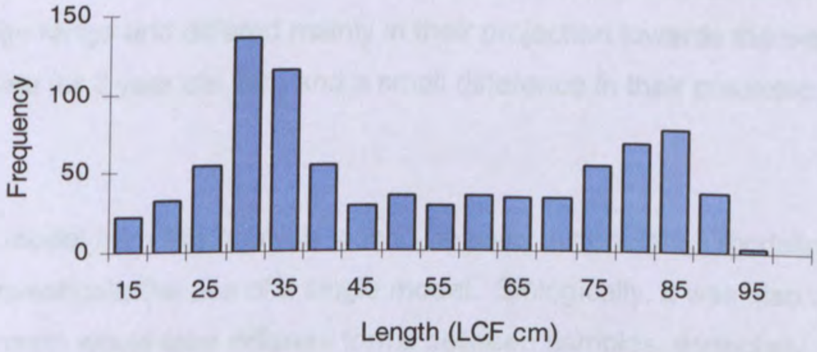


Fig. 7.1. Frequency distribution of snapper used in the growth analysis based on age and length.

7.2.1.1 Growth models

The data were initially fitted using Schnute's general model (Eq. 15 of Schnute (1981)

$$Y(t) = \left[y_1^b + \left(y_2^b - y_1^b \right) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{\frac{1}{b}} \tag{7.1}$$

where $Y(t)$ = fish size at age t

τ_1, τ_2 = fixed ages of a young (1) and old (2) fish

y_1, y_2 = size at ages τ_1, τ_2

a, b = estimated parameters

The fitting process requires selection of ages τ_1 and τ_2 (near the minimum and maximum ages for which data are available) and then estimation of a, b, y_1 and y_2. The resulting estimates of a and b define the model type which best fit the data (see Table 1 in Schnute (1981). In this study, τ_1 and τ_2 were chosen as 2 and 30 years respectively.

The initial analysis treated the 1991 and 1994 samples separately. The two estimates of a were both positive but estimates of b were negative and positive for 1991 and 1994 respectively (see Results). This suggested that the data from each year were best described by two different growth models – a Richards model for 1991 and a generalized von Bertalanffy model for 1994. However, the two curves were similar for much of the age range and differed mainly in their projection towards the x-axis (beyond the data for 2 year old fish) and a small difference in their predicted asymptotic length.

As the growth model from this analysis was to be used in population modeling, it was preferable to investigate the use of a single model. Biologically, it was also considered unlikely that growth would take different forms between samples, especially considering the overlap of 28 years in the two datasets. Therefore, the Schnute model was re-estimated for the combined dataset and compared to the results obtained from treating the two datasets separately.

The Schnute model (using parameters a, b, y_1 and y_2) does not incorporate a term for seasonal growth. There were two reasons for wishing to incorporate seasonal growth in the analysis: the water temperature range is significant in the study region and it was considered likely that demonstrable seasonality would exist. Secondly, the population model required calculation of length at age at time periods other than whole years and this would be better estimated if seasonal growth was incorporated.

Application of the Schnute model led to the use of a generalized von Bertalanffy growth model (see Results) where the length (Y) of fish i at age t is

$$Y(t_i) = L_\infty \left(1 - e^{-K(t-t_0)}\right)^p \qquad (7.2)$$

where L_∞ = asymptotic size (cm)
K = the rate at which length approached L_∞
t = age (years)
t_0 = theoretical age (years) at zero length
p = exponent to the specialized von Bertalanffy model (where $p = 1$) and $=1/b$ where b is defined in 7.1

Seasonality can be incorporated by adding a sinusoidal term to the exponent within the brackets of Eq. 7.2. The full growth model therefore becomes

$$Y(t_i) = L_\infty \left(1 - e^{-K\left(t - t_0\right) + \frac{\mu}{2\pi}\left[\sin\left(2\pi\left(t - \omega\right)\right) - \sin\left(2\pi\left(t_0 - \omega\right)\right)\right]}\right)^p \qquad (7.3)$$

where μ = amplitude of the seasonality
ω = the time of year of maximum growth

In population modeling, $\mu > 1$ leads to a decrease in length at the time of slowest growth (McGarvey 2000) and μ was therefore constrained to be ≤ 1. Schnute (1981) demonstrated a difficulty in estimating parameters in Eq 7.2 which occurs when p tends to positive infinity and t_0 tends to negative infinity. The minimization search can continue endlessly without finding an endpoint. To overcome this problem (which occurred with initial iterations), the exponent p was fixed at $1/b$ (= 3.210764) where b (= 0.311452) was estimated from estimations of Eq. 7.1.

7.2.1.2 Parameter estimation

Schnute's model was fitted by minimising least squares while the fitting of the generalised von Bertalanffy curve was fitted using maximum likelihood. The advantage of using least squares in the exploratory model fitting was the computational advantage of not needing to specify a form for the likelihood standard deviation. Additionally, the two methods are likely to lead to similar results as likelihoods are maximised when squares are minimised (Kimura 1980). Schnute's original development and testing of his general model also used least squares fitting methods (Schnute 1981).

Maximum likelihood was used for fitting the von Bertalanffy growth curve because estimates converge in probability to the correct value (i.e. are consistent), are asymptotically normal and asymptotically attain the smallest possible variance (Kimura 1980). Once the appropriate growth model was identified, the model parameters (L_∞, K, t_0, μ and ω) were estimated using the normal likelihood function L

$$L = \frac{1}{\sqrt{2\pi}\,\sigma(t_i)} \exp\left[-\frac{1}{2}\left(\frac{Y_i - \bar{Y}(t_i)}{\sigma(t_i)}\right)^2\right] \tag{7.4}$$

where $\bar{Y}(t_i)$ is determined from Eq. 7.3.

A number of different forms of the likelihood standard deviation $\sigma\,(t_i)$ were modeled:

$$\sigma = s * t_i \tag{7.5}$$

$$\sigma = s * t_i^{\,c} \tag{7.6}$$

$$\sigma = s\,(1 - e^{-c\,t_i}) \tag{7.7}$$

$$\sigma = \min\,(s\,t_i,\ c\,) \tag{7.8}$$

$$\sigma = s + c\,t_i \tag{7.9}$$

where s and c are parameters to be estimated. The linear form (Eq. 7.9) maximized the log-likelihood and was used for all estimations.

The parameters were estimated by maximizing the sum of the log-likelihoods of Eq. 7.4 using the Solver routine in Excel. The standard deviations of each parameter were calculated using simulations. 100 new data sets were generated using the likelihood estimates and the likelihood standard deviation. The parameters were then re-estimated for each new dataset using Solver. Standard deviations for each parameter were calculated directly from the 100 new estimates.

7.2.1.3 Testing between models

A number of different methods have been used to test between the fits of growth models and have, to some degree, been dictated by the estimation method. For example, Schnute (1981) and Kimura (1980) (using least squares estimation methods) based their tests on the ratio of sums of squares generated by each model. Schnute (1981) used the ratio of the variances (sum of squares) to test between the four parameter general model and a three parameter sub-model and tested the result against the F-distribution. He noted that the test statistic would be F-distributed if the models were linear, or approximately F-distributed for non-linear models for large samples. Use of this test for non-linear models should therefore be considered indicative rather than a rigorous analysis. Kimura (1980) showed that –N * the ratio of the sums of squares (where N is the sample size) would have asymptotically a χ^2 distribution with degrees of freedom equal to the number of parameters fixed.

Francis (1988) and Francis and Winstanley (1989) used maximum likelihood methods to estimate growth of *P. auratus* and used the likelihood-ratio test to compare the improvement in fit following the addition of extra parameters to the growth model. Francis (1988) noted that twice the difference between the log likelihood function values with and without the additional parameters is asymptotically distributed according to a χ^2 distribution with *n* degrees of freedom. Thus an increase of 1.92 and 3.00 is necessary for the addition of one and two parameters respectively at the 5% significance level.

Two tests were conducted in this analysis. The first compared the fit of separate models to the 1991 and 1994 models to the fit of a single model to the combined datasets (in both cases Schnute general models), both of which were fitted using least squares. Kimura's statistic was used and tested against the χ^2 distribution with four degrees of freedom (= four parameters with equal values in each population).

The second test compared the fit of generalized von Bertalanffy curve before and after the addition of the seasonal growth parameters μ and ω. These curves were fitted using maximum likelihood methods and the improvement in model fit for the addition of two extra parameters must therefore be greater than 3.00 to accept the alternative hypothesis of a better fit using seasonal growth.

7.2.2 Tagging data analysis

The snapper tagging program from 1987 to 1992 was described in detail in Chapter 6. Of the total of 646 snapper tagged and recaptured in Spencer Gulf, Gulf St Vincent and waters outside of the Gulfs, 466 were either tagged or recaptured in northern Spencer Gulf (NSG). 383 records included sufficient information on length and date at release and recapture to calculate growth increments. Of these, 361 were tagged and recaptured in NSG, 9 were tagged in NSG but recaptured elsewhere and 13 were tagged elsewhere but recaptured in NSG. All of these records were used in the analysis. There was an additional 15 records from fish which were recaptured more than one time, but only the data from the first recapture were used.

The growth model (see Section below) requires a choice of two release lengths that are well represented by the data. The tagged fish were predominantly small to medium sized between 20 and 40 cm LCF (Fig. 7.2). Less than 10% of the fish tagged exceeded 40 cm LCF, but did include fish of up to 81 cm LCF.

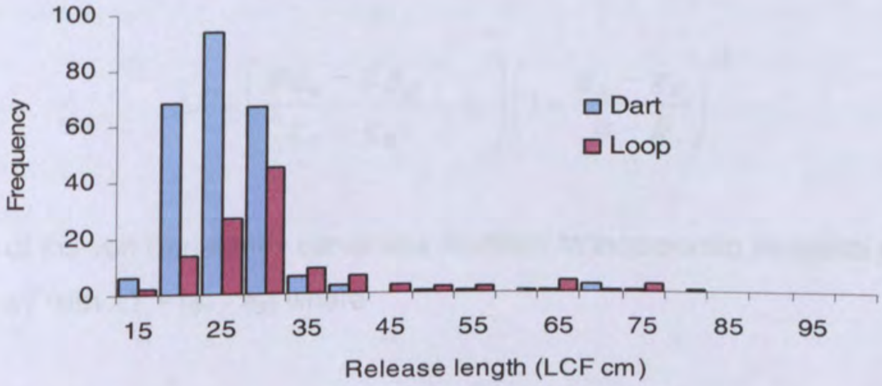


Fig. 7.2. Length of snapper at time of release for fish used in growth analysis.

7.2.2.1 Growth models

For tag recapture data, the von Bertalanffy growth function can be rewritten as

$$\Delta L = \left(L_{\infty} - L_1\right)\left(1 - e^{-K\Delta T}\right) \tag{7.10}$$

where ΔL and ΔT refer to the difference in length and time between recapture and release respectively, and L_1 is length at release.

To address the limitations of the von Bertalanffy parameters with tagging data, Francis (1988) re-parameterised the function so that

$$L_{\infty} = \frac{\beta g_{\alpha} - \alpha g_{\beta}}{g_{\alpha} - g_{\beta}} \tag{7.11}$$

and

$$e^{-K} = 1 + \left(\frac{g_{\alpha} - g_{\beta}}{\alpha - \beta}\right) \tag{7.12}$$

where g_{α} and g_{β} are the mean annual growth rates of fish of lengths α and β respectively. The lengths α and β are chosen arbitrarily but should be well defined by the data in tag recapture dataset.

Using these parameters, Eq 7.10 can be rewritten as

$$\Delta L = \left(\frac{\beta g_{\alpha} - \alpha g_{\beta}}{g_{\alpha} - g_{\beta}} - L_1\right)\left(1 - \frac{g_{\alpha} - g_{\beta}}{\alpha - \beta}\right)^{\Delta T} \tag{7.13}$$

This form of the von Bertalanffy curve was modified to incorporate seasonal growth by replacing ΔT with $\Delta T + (\phi_1 - \phi_2)$ where

$$\phi_i = \mu\left(\frac{\sin\left(2\pi\left[T_i - w\right]\right)}{2\pi}\right) \text{ for } i = 1, 2 \qquad \text{(Francis 1988)} \tag{7.14}$$

where μ and ω have the same definition of amplitude and time of year as described in Sect 7.2.1.1. μ was similarly constrained to be ≤ 1.

Francis (1988) added five further parameters to the growth model. The first was a parameter to estimate the variability around the estimate of mean growth. He assumed that growth of a fish L_1 over time ΔT is normally distributed with mean μ and standard deviation σ. Growth variability is therefore defined by σ and he proposed a number of potential linear and non-linear relationships between mean growth (u) and σ

$$\sigma = \nu\mu \tag{7.15}$$

$$\sigma = \nu\mu^{t} \tag{7.16}$$

$$\sigma = t\,(1 - e^{-\nu\mu}) \tag{7.17}$$

$$\sigma = \min\,(\nu\mu,\ t) \tag{7.18}$$

These forms were sequentially tested to determine which best described growth variability for snapper in South Australia.

The second parameter (p) was the probability of an outlier caused by transcription errors. This parameter was introduced to provide a means of minimising the effect of "unusual" data while allowing inherent (and assumedly true) variability to be estimated. To incorporate p into the model, a parameter R describing the range of length increments (maximum minus minimum increments) was also required.

The final two parameters provide an estimate of measurement error, which combines errors associated with the measurements taken at the times of release and recapture of the fish. The parameter cannot distinguish between the two events and is therefore a net error. The measurement error is assumed to be normally distributed with a mean m and standard deviation s. The full set of parameters and their symbols are summarised in Table 7.1.

Table 7.1 Parameters used in growth model based on tagging data.

Descriptor	Symbol and unit
Mean growth	g_α (cm.year^{-1}) g_β (cm.year^{-1})
Amplitude of seasonal growth	μ
Time of year of maximum growth	ω (year)
Growth variability	ν
Net measurement error (standard deviation)	s (cm)
Net measurement error (mean)	m (cm)
Outlier contamination	P

7.2.2.2 Parameter estimation

The model was fitted using a log-likelihood function of

$$\lambda = \sum_i \log\left[(1-p)\lambda_i + \frac{p}{R}\right] \tag{7.19}$$

where the normal likelihood function is

$$\lambda_i = \frac{1}{\sqrt{2\pi\left(\sigma^2 + s^2\right)}} \exp\left(\frac{-\left(\Delta L_i - u_i - m\right)^2}{2\left(\sigma^2 + s^2\right)}\right) \tag{7.20}$$

The GROTAG program developed by Francis (1988) was converted into MS Excel format by Dr Rick McGarvey, SARDI, and this platform was used for these analyses. Log likelihood was maximised using the Solver routine in Excel.

For the combined tagtype data, g_α and g_β were chosen as 25 cm and 35 cm LCF respectively based on the length at time of release (Fig. 7.2),. The initial model specification used the minimum of three parameters (g_α, g_β and s). Extra parameters were then added individually to assess the relative effect of each on the log-likelihood. The final growth model was constructed by adding the additional parameters sequentially in order of their relative effect, which was determined by the difference in log-likelihood between the three parameter model and the model including each additional parameter.

The data were then re-analysed to determine whether any difference existed between the growth rates (g_α, g_β) of fish tagged with loop or dart tags (hereafter called the tagtype model), while maintaining common estimates of the other growth model parameters. Of the 371 recapture data used in the previous analysis, 120 and 251 were tagged with dart and loop tags respectively.

The starting point of this re-analysis was the best fit model of the combined data. The initial tagtype model estimated independent g_{25} and g_{35} for each tagtype but made a common estimate for other parameters. The residuals of this model suggested that snapper tagged with loop tags exhibited greater growth variability and so a second model was specified allowing growth variability ν to vary between the tagtypes in addition to g_{25} and g_{35}.

7.2.2.3 Testing between models

The improvement of fit of models containing additional parameters was tested using the likelihood ratio test (LRT) (Kimura 1980). A significantly better fit is obtained by an improvement in log likelihood of 1.92 or 3.00 for the addition of 1 or 2 parameters respectively (Francis 1988).

Francis (1988) noted that the LRT may be used where there are no outliers (*p* = 0) and proposed a series of calculations using a range of *p* and *R* where outliers exist. However, the process is cumbersome and an alternative approach was used here. Where *p* > 0, the individual datum with the lowest log-likelihood was deleted from the dataset and the model parameters re-estimated. This process was repeated until *p* = 0. That is, outliers were objectively determined from their log-likelihood and removed from the analysis.

The process for assessing the significance of improvements in fit between the combined data and tagtype models is outlined in Francis and Winstanley (1989). Suppose that the log likelihood of model 1 is greater than model 2 (ie model 1 is a better fit than model 2) and yields a difference ΔLL (ie $LL_1 - LL_2 = \Delta LL$). 100 datasets were generated using the original L_1, T_1 and T_2 and using the parameters estimated for model 2 (the poorer fit model). The datasets derive their variability from the two parameters σ and s – specifically, by adding a random normal number with mean 0 and standard deviation $(\sigma^2 + s^2)^{0.5}$.

The parameters and maximum log likelihood were then re-estimated for each dataset using both models. The difference between log likelihoods was calculated for each dataset and compared with ΔLL. If more than 95% of the simulated log likelihood differences $< \Delta LL$, then model 1 is considered to be a significantly better fit (at the 5% significance level).

Where the results suggest a significantly better fit, the process was repeated to assess whether the original data are consistent with model 1. This time, 100 new datasets were generated based on L_1, T_1 and T_2 but this time using the parameters of model 1 (the better fit model). If ΔLL falls outside of 95% of the simulated log likelihood differences, model 1 was rejected (at the 5% significance level). The standard deviations of the best fit model were calculated from the 100 simulated datasets.

7.3 Results

The results of the age length and tagging analyses are first described separately in this section and are later compared in the Discussion.

7.3.1 Age length

The Schnute general model produced estimates for *a* and *b* which suggested that different growth models would be appropriate for each of the 1991 and 1994 samples (Table 7.2). The 1991 sample gave a positive estimate for *a* and a negative estimate for *b*, suggesting use of the Richards growth curve (or if further testing showed that *b* was not significantly different to 0, a Gompertz curve could be used (Schnute 1981)). The 1994 estimates produced positive estimates for *a* and *b*, suggesting a generalized von Bertalanffy curve.

Table 7.2 Parameter estimates for the Schnute general model using both separate data from the 1991 and 1994 samples, and for the combined datasets. RSS = residual sum of squares

		Estimates	
	Parameters	Separate	Combined
1991	y1	20.08	18.32
	y2	87.82	89.77
	a	0.227	0.195
	b	-0.115	0.311
1994	y1	17.75	
	y2	90.05	
	a	0.199	
	b	0.336	
	RSS[1]	29359	29564
	χ^2		5.619
	df		4
	P		0.2294

While separate growth models are feasible mathematically, this is unlikely to be biologically realistic, particularly as the two samples had 28 overlapping yearclasses - all yearclasses of the 1991 sample were re-sampled in the 1994 sample. It is likely therefore that the different estimates for *a* and *b* which determine the growth model are mathematical artifacts rather than real differences between the two samples. The curves generated by the separate estimates of parameters show differences before 2 years of age where the curves are not supported by data, and in the asymptotic length (Fig. 7.3).

Re-estimation of the parameters using the combined data produced positive estimates of *a* and *b* indicative of the generalised von Bertalanffy curve (Table 7.2). The sum of squares did not differ significantly from the fit of the separate curves and so the single growth curve was accepted as an adequate description of the data. In this form, the parameter *a* is equivalent to *K* in the von Bertalanffy growth curve (Eq. 7.2) and 1/*b* is the exponent.

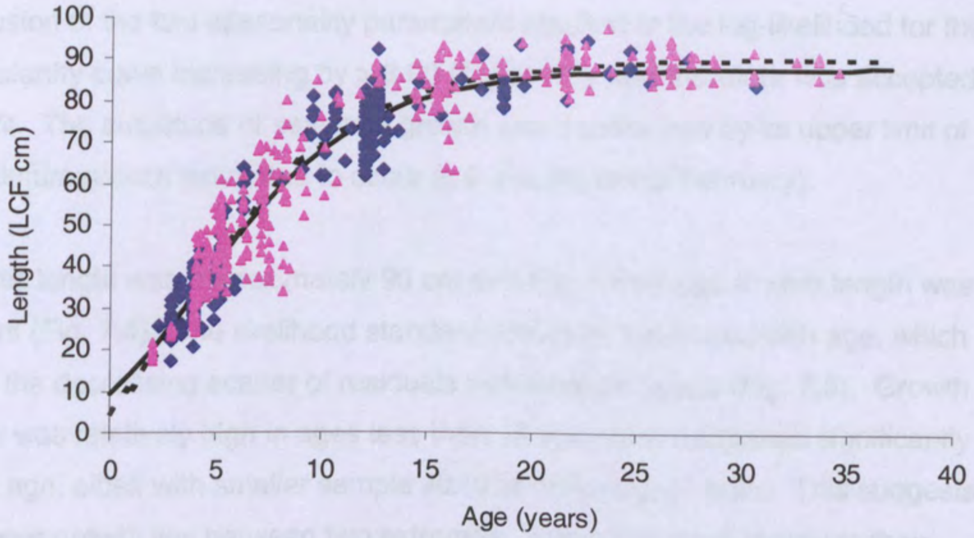


Fig. 7.3 Separate growth curves (1991; solid line and 1994; dashed line) for the 1991 (◊) and 1994 (Δ) snapper samples using the general Schnute growth model and parameters estimated by least squares.

Table 7.3 Estimates of the maximum likelihood parameter for the generalised von Bertalanffy growth curve with and without seasonality.
Standard deviations are calculated from the estimates of maximum likelihood from 100 simulated datasets generated from the original estimates and likelihood standard deviation.

Parameter	No seasonality Estimates	Seasonality Estimates	Simulations Mean	 SD
L_∞ (cm)	90.00	90.19	90.149	0.537
K	0.197	0.194	0.194	0.005
t_0 (years)	-2.742	-2.860	-2.853	0.128
μ	0^1	1.000^2	0.916	0.164
ω (years)	0.152	0.151	0.160	0.077
Exponent [3]	3.211	3.211	-	-
s_0	7.218	7.104	7.138	0.248
s_2	-0.124	-0.117	-0.122	0.017
Log-Likelihood	-2601.0	-2595.1		

[1] fixed at 0 (= no seasonality)
[2] constrained $0 \leq \mu \leq 1$
[3] fixed

The inclusion of the two seasonality parameters resulted in the log-likelihood for the von Bertalanffy curve increasing by > 3.00 (Table 7.3), and therefore was accepted as a better fit. The amplitude of seasonal growth was constrained by its upper limit of 1, with maximum growth estimated to occur at 0.1 years (early February).

Asymptotic length was approximately 90 cm and theoretical age at zero length was – 2.86 years (Fig. 7.4). The likelihood standard deviation decreased with age, which reflected the decreasing scatter of residuals with increasing age (Fig. 7.5). Growth variability was relatively high in ages less than 15 years but decreased significantly after that age, albeit with smaller sample sizes at these higher ages. This suggests that snapper growth lies between two extremes. Some fish grow rapidly to their asymptotic size but then show little further growth. For example, some snapper were approaching their asymptotic size of 90 cm LCF at 12 years of age. On the other hand, some fish were only approaching 90 cm LCF at > 25 years. Thus in northern Spencer Gulf, it is the rate of growth to $L\infty$, or K, that is highly variable.

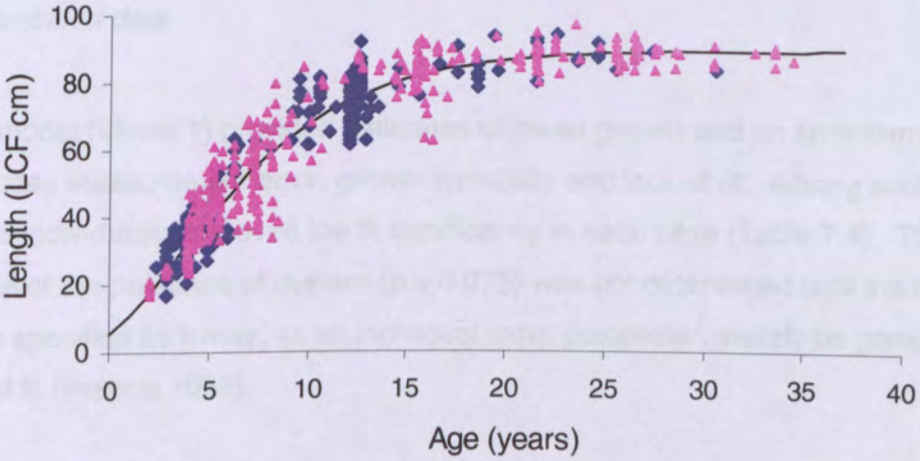


Fig. 7.4 Growth curve for the combined 1991 (◊) and 1994 (Δ) snapper samples using the general Schnute growth model and parameters estimated by maximum likelihood.

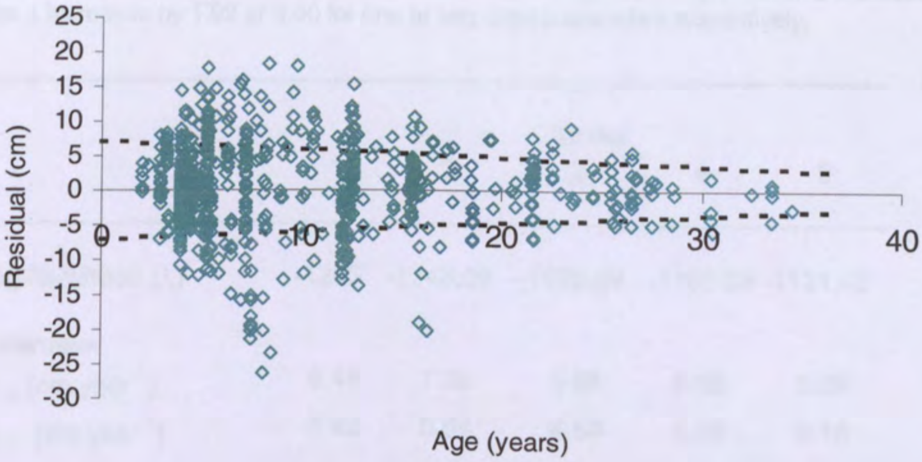


Fig. 7.5 Residuals of the generalised von Bertalanffy curve (combined data). Maximum likelihood standard deviation is shown by the dashed lines.

7.3.2 Tagging

7.3.2.1 Combined data

The base model (Model 1) provided estimates of mean growth and an error term *s* which includes measurement error, growth variability and lack of fit. Adding additional parameters individually improved the fit significantly in each case (Table 7.4). The significance of the presence of outliers ($p = 0.075$) was not determined until the full model was specified as it may, as an individual extra parameter, merely be generated by a lack of fit (Francis 1988).

The largest improvement in fit (excluding outliers) was growth variability (Table 7.4). The three more complex forms of growth variability, which incorporated an extra parameter *t*, showed no significant improvement in fit (Table 7.5) and the simpler linear relationship (Eq. 7.6) was therefore retained.

Table 7.4 Growth parameter and maximum log likelihood estimates for assessing the improvement in fit of individual parameters to the base model (1).

The shaded estimates are those added in each model. Significant improvements are accepted where λ increases by 1.92 or 3.00 for one or two extra parameters respectively.

	Model				
	1	2	3	4	5
Log-likelihood (λ)	-1203	-1148.99	-1190.09	-1193.03	-1121.42
Parameter					
g_{25} (cm.year^{-1})	6.48	7.36	5.04	6.59	5.59
g_{35} (cm.year^{-1})	5.92	6.64	4.69	5.98	5.16
u (year)	0			1.000[1]	
w (year)	0			0.085	
ν	0	0.456			
s (cm)	5.596	3.49	5.411	5.452	3.426
m (cm)	0		2.259		
P	0				0.075

[1] constrained $0 \leq \mu \leq 1$

Table 7.5 Parameter estimates and maximum log-likelihoods for four growth variability forms when tested without additional model parameters.

The growth variability forms in Models 1 – 4 are described in Equations 6.6 to 6.9 respectively.

	Model			
	1	2	3	4
Log-likelihood (λ)	-1148.99	-1148.79	-1148.82	-1148.6
Parameter				
g_{25} (cm.year^{-1})	7.36	7.39	7.39	7.35
g_{35} (cm.year^{-1})	6.64	6.67	6.67	6.64
ν	0.456	0.312	-0.023	0.464
T		1.139	16.696	11.332
s (cm)	3.49	3.599	3.573	3.472

The full model was sequentially built by adding parameters in the order of growth variability, mean measurement error, seasonal growth and outlier contamination. In each case, the addition of extra parameters provided a significantly better fit (Table 7.6). Model V (p = 0.057) suggests that outliers remained within the dataset. The sequential removal of 12 datapoints (ie a final dataset of 371 records) and re-analysis, resulted in a model without outliers and a significant improvement in fit.

Table 7.6 Parameter estimates and log-likelihoods of growth models (1, II – V) adding additional parameters sequentially.
The shaded estimates are those added in that Model. All additional parameters provided a significantly better fit (λ increased by > 1.92 or 3.00 for one or two extra parameters respectively). Model VI shows parameter estimates and log-likelihood for the dataset without outliers (see text for method of removal of data).

	Model					
	1	II	III	IV	V	VI
N			383			371
Log-likelihood (λ)	-1203	-1148.99	-1128.77	-1106.89	-1053.07	-959.28
Parameter						
g_{25} (cm.year^{-1})	6.48	7.36	5.24	6.04	5.255	5.291
g_{35} (cm.year^{-1})	5.92	6.64	4.77	5.47	4.982	5.048
u (year)	0			1.00[1]	1.000[1]	1.000[1]
w (year)	0			0.04	0.037	0.022
v	0	0.456	0.628	0.600	0.404	0.433
s (cm)	5.596	3.492	3.210	2.600	2.018	2.148
m (cm)	0		2.206	1.378	1.286	1.314
p	0				0.052	0

[1] constrained $0 \leq \mu \leq 1$

7.3.2.2 Separate tagtype data

Model VI was used as the base model to compare the effect of estimating separate growth parameters for fish tagged with dart and loop tags. The first re-analysis allowed g_{25} and g_{35} to vary between tagtypes but produced common estimates for other parameters. The residuals of this model suggested that growth variability for loop tagged fish may have been greater than for dart tagged fish (Fig. 7.6). The Model was therefore re-estimated allowing g_{25}, g_{35} **and** ν to vary between tagtypes (Table 7.7).

Table 7.7 Parameter estimates and maximum likelihood of a growth model allowing separate g_{25}, g_{35} and ν for dart and loop tagged snapper.

	Model		
	VI	Tagtype	
		dart	loop
n	*371*	*120*	*251*
Log-likelihood (λ)	-959.28	-951.12	
Parameter			
g_{25} (cm.year^{-1})	5.291	6.789	4.883
g_{35} (cm.year^{-1})	5.048	6.147	4.942
u (year)	1.000[1]	1.000[1]	
w (year)	0.022	0.026	
ν	0.433	0.320	0.452
s (cm)	2.148	2.129	
m (cm)	1.314	1.176	
p	0		

[1] constrained $0 \leq \mu \leq 1$

The significance testing by simulation showed that this new tagtype growth model was a significantly better fit ($P < 0.01$) than the combined data model, and there was no evidence to reject the tagtype model ($P = 0.63$). The results of the 100 simulations are shown in Table 7.8.

Table 7.8 Results of 100 simulations of the snapper tagging data using the parameters of the tagtype model. D = dart tagged fish, L = loop tagged fish

	Parameter	Model estimate	Simulation estimates mean	SD
Dart tags				
	g_{25} D	6.74	6.62	0.50
	g_{35} D	6.11	5.98	0.40
	ν D	0.32	0.35	0.07
Loop tags				
	g_{25} L	4.82	4.74	0.35
	g_{35} L	4.97	4.84	0.29
	ν L	0.45	0.47	0.05
Common				
	s	2.13	1.83	0.15
	m	1.16	1.32	0.23
	μ	1.00	1.00	0.18
	ν	0.02	0.02	0.03

The growth rate estimates from the tagtype model are much higher for dart tagged fish than for loop tagged fish (Table 7.8). Estimates for 25 and 35 cm dart tagged snapper are 40% and 23% higher than for loop tagged fish, suggesting a significant adverse effect of the latter tags. The estimates for dart tagged fish convert to von Bertalanffy estimates of $K = 0.066$ and L_∞ of 130 cm (where L_∞ and K are derived from Eqs 7.11 and 7.12 respectively).

The estimates for loop tagged snapper also suggest that the growth rates for 25 cm fish are slightly less than those for 35 cm fish (Table 7.7). Pairwise comparison of the simulation data shows that this difference was evident in 67% of estimates and is significant (one tailed paired t-test; $P < 0.01$). This result is implausible in terms of describing the growth of a species by a von Bertalanffy curve i.e. it describes a function of increasing growth rate with size. However, the results may indicate that the adverse effect of the loop tags was on growth rates is more severe for the smaller fish. The residuals from this model show no pattern when plotted against expected growth, length at tagging or time at liberty (Fig 7.6).

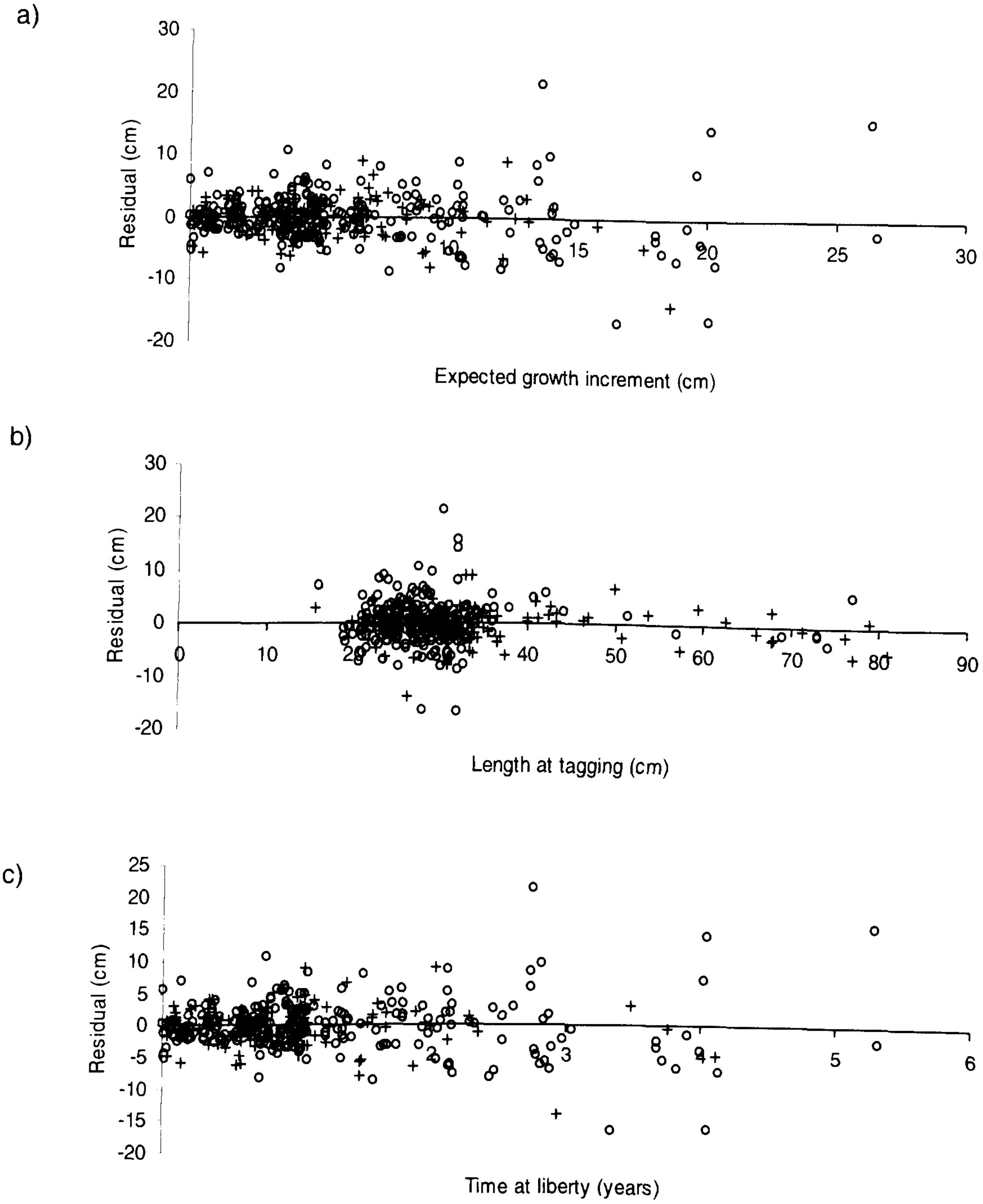


Fig. 7.6 Residuals of the tagtype model (dart tags o, loop tags +) shown plotted against a) expected growth increment, b) length at time of tagging and c) time at liberty

7.4 Discussion

The age length and tagging datasets have provided a rich source of data for investigating the growth of snapper in northern Spencer Gulf. However, growth rates calculated from age length and tagging data describe growth in two different ways and are not directly comparable (Francis 1988). For a standard time interval of (say) one year, the former describes the mean annual growth of fish from age t_1, while the latter describes mean annual growth from length l_1 (independent of age). Although each set of growth estimates could be treated separately, our understanding of growth (and the relative benefits of the data sources) would be greatly enhanced by the ability to compare the respective results.

To enable this comparison, the estimates of one analysis need to be converted to the same base (i.e. age or length) as the other. The tagging data (length based) does not contain any direct measure of age and so these results cannot be converted to compare to growth derived from age/length estimates. However, the age/length data clearly contains length information and so can be compared to growth derived from tagging derived (length based) growth. To do this, the mean annual growth of snapper after they have reached mean sizes of 25 and 35 cm (the equivalent of g_{25} and g_{35}) must be found from the age length curve. This can be done by calculating the age of fish of mean lengths 25 and 35 cm from Eq. 6.3 and, by adding 1 year, mean growth for the following year can be calculated from the same equation.

Snapper from northern Spencer Gulf reached a mean length of 25 cm at age 3.00 years and showed mean growth of 7.7 cm in the following year. Mean length of 35 cm was reached at age 4.17 years and mean annual growth was estimated at 7.2 cm. By comparison, g_{25} and g_{35} were estimated at 6.8 cm and 6.1 cm respectively for the dart tagged snapper (the loop tagged snapper estimates did not conform to von Bertalanffy growth and are not considered in this comparison). These estimates are 11.7% and 15.3% lower than those derived from the age length data.

The differences in the results may be explained by factors relating to the age length or tagging sample data and/or their respective analyses. Errors in the age length data (ageing errors, measurement errors) are considered less likely to be the cause. The precision of age estimates between independent readings was high and there was no consistent bias evident (Fig. 3.6 in this study, McGlennon et al. 2000). Furthermore, length measurements were taken by research staff in good working conditions within processing plants and the age length analysis provided a biologically reasonable set of growth estimates for this species. For example, the asymptotic length L_∞ of 90.2 cm fits well with the maximum length of snapper observed during sampling.

The analysis of tagging data, on the other hand, estimated a very low value for K and an L_∞ of 130.6 cm, which is at least 30% larger than any snapper recorded in this (or other South Australian) studies. And yet the residuals of the tagtype model suggest that this was an appropriate fit for the tagging data. There are two potential explanations for the apparent poor estimates from the tagging data: 1) the size range of fish tagged was too limited to provide an adequate description over the whole size range in the population and 2) the possibility that tagging adversely affected growth.

Only 13% of all snapper tagged were > 35 cm LCF at initial capture, due to a number of factors: the relative abundance of small fish, their attractiveness to recreational and commercial fishers for tag and release as they are less than the legal minimum length, the reluctance to release large fish after capture and the loss of vigor of large fish (relative to small ones) after capture. This significant weighting towards small fish in the data would have biased the estimation procedure towards these data. However, re-analysis using a scaling factor (scaling the residuals of the larger fish to proportionally weight the number of larger fish to be equal to the number of smaller fish in the sample) failed to improve the estimates of K and L_∞.

The second potential explanation is that tagging adversely affected growth. The growth estimates separated by tagtype clearly showed a difference between fish tagged with dart and loop tags. The growth estimates from fish tagged with loop tags did not conform to von Bertalanffy growth suggesting that growth (at least in comparison to dart tagged fish) was severely affected. Although such fish were recaptured up to 5.8 years after release, they often showed a chronic open wound up to 5 mm around the tag entry. Such a chronic injury was not evident in dart tagged fish.

Juvenile *P. auratus* (15 – 21 cm LCF) tagged with 4.5, 6 and 9 cm streamer length Hallprint dart tags have previously been held in captivity without apparent effects on growth or survival (Quartararo and Kearney 1996). Minor tag wounds were still evident at the conclusion of that experiment but even those with a more severe wound (2mm abscess around the tag entry) were observed feeding and considered to be in good condition. (Quartararo and Bell 1992) also found no effect of passive implantable transponder tags on weight gain of juvenile *P. auratus.* However, adverse effects on growth from tagging have been recorded in other studies. For example, McFarlane and Beamish (1990) reported the results of a tagging program on sablefish *Anoplopoma fimbria* tagged with Floy FD-68 anchor tags, where the effect of tags on growth was manifested in delays of up to 25% in the time to reach maturity. Acoustic transmitters have been shown to affect the growth of Atlantic salmon *Salmo salar* (Robertson et al. 2003; Lacroix et al. 2004), sole *Solea solea* and juvenile seabass *Dicentrarchus labrax* (Anras et al. 2003), as have archival tags for Pacific bluefin tuna *Thunnus orientalis* (Itoh et al. 2003) but coded wire tags were found to have no effect on growth of coho salmon *Oncorhynchus kisutch* (Blankenship and Thompson 2003).

The growth rates estimated from the tagging program were affected by either or both of the unrepresentative length sample of fish tagged and the physical effects of tagging on growth. Furthermore, the latter effects were significant on loop tagged *P. auratus*, indicating that these tags are inappropriate for use with this species.

7.4.1 Seasonal growth

The analyses using age length and tagging data consistently demonstrated seasonality associated with growth (Fig. 7.7). In both analyses, the amplitude parameter was estimated at its upper constraint of 1 indicating significant seasonality. The water temperature in northern Spencer Gulf varies from approximately 12^0 in late winter to $>25^0$C in late summer. Thus, seasonal growth was not unexpected. The time of maximum growth was estimated at late February by the age length model and early January by GROTAG (Fig. 7.7). This coincides with maximum water temperatures in the study region.

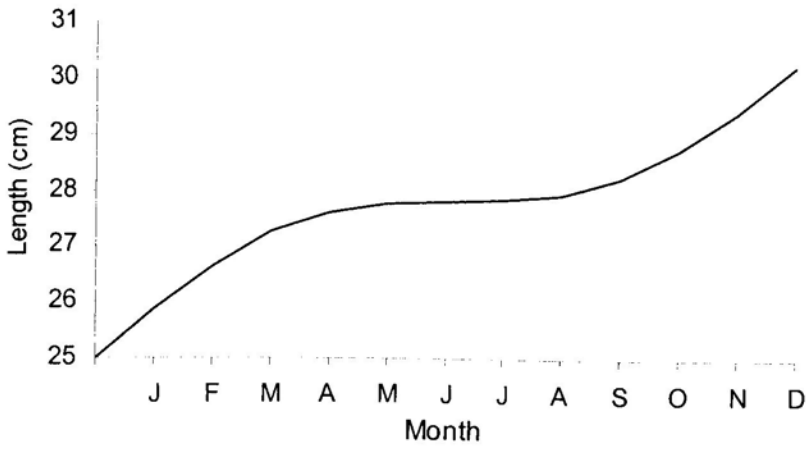


Fig. 7.7 Example of seasonal growth of a snapper of 25 cm fork length based on growth rates estimated by GROTAG using the combined dataset.

7.4.2 Growth variability and measurement error

GROTAG also provided useful estimates of growth variability (ν) and measurement error (m). It is clear from the scatter in the age length data (Figs. 7.4 and 7.5) that a high degree of variability exists in the individual growth of *P. auratus.* GROTAG directly estimated this variability as the coefficient of variation of the growth increment. The analysis of growth by tagtype showed lower variability for dart tagged fish (0.320) than with loop tagged fish (0.452). Both values are much higher than those reported for *P. auratus* in Victoria, Australia ($\nu = 0.18$; Model 4 Table 2, Francis and Winstanley 1989), where the $\approx 12^0$C range of water temperatures (www.earthsci.unimelb.edu.au) in Port Phillip Bay is similar to that in northern Spencer Gulf.

A recent study modeled the growth of the tropical emporer *Lethrinus mahsena* using a nonlinear random effects model to estimate individual growth variability (Pilling et al. 2002). The model assumed that individual growth parameters were samples from a multivariate population of growth parameters compared to the standard approach which characterizes the joint distribution of growth parameter estimates. The growth parameter estimates were similar for each approach but the variances of estimates were much lower with the approach used in the study.

The measurement error of 1.176 cm is similar to that reported for *P. auratus* in Port Phillip Bay ($m = 1.3$ cm; Model 4 Table 2, Francis and Winstanley 1989) although those authors caution against literal use of that estimate due to their low sample sizes. The measurement error parameter reflects net error during initial release and subsequent recapture. In this study, commercial and recreational fishers were involved, as well as research staff. Although some training was provided to fishers prior to tagging, it may have been expected that measurement error would have been higher still given the range of skills and measuring conditions encountered during the program.

7.4.3 Growth comparisons with other studies

The growth curves from previous South Australian studies using tagging data and ages based on scale readings are compared to the curve based on otolith ages developed in this study in Fig. 7.8. The maximum age recorded from scale ageing work was 23 years but those curves have been extrapolated to match the maximum age recorded from otoliths (Chapter 3). The curve depicting growth based on ages derived from otoliths clearly shows a faster rate of growth towards the asymptotic length than other growth curves and a greater tendency to asymptote at a maximum length than curves based on ages from scale readings.

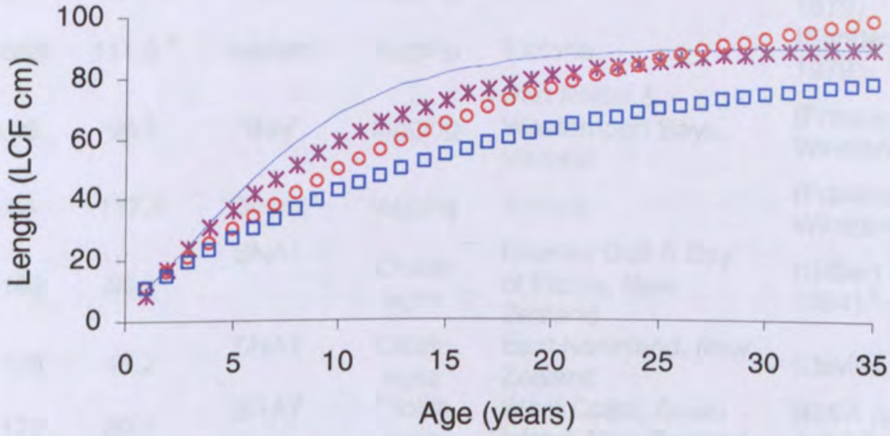


Fig. 7.8 Comparative growth curves for South Australian snapper.
Based on otolith ages from this study (solid line), and scale ages (O and □) and tag recapture data (✳) reported by Jones (1984, 1987).

Estimates of growth parameters of *P. auratus* from other southern hemisphere studies are summarized in Table 7.9. The northern Spencer Gulf snapper reach a similar maximum length to the “Bay” and “eastern” Victorian snapper but are significantly larger than New Zealand snapper. The rate of growth at which they approach maximum length is the fastest reported from these studies.

7.4.4 Conclusions

This study has provided a comparative analysis of the growth data available from two independent sources through the period from 1988 – 1996. It is concluded that the growth rates based from the age length keys derived from the combined 1991 and 1994 otolith samples provide the basis for describing growth in *P. auratus* in northern Spencer Gulf. These rates were used to estimate mean length at age in the population modeling described in Chapter 8.

Table 7.9 Growth parameter estimates from other studies of *P. auratus* in the southern hemisphere.

t_0 *(year)*	*K* *(yr^{-1})*	L_∞ *(LCF cm)*	Stock	Method	Location	Source
-	0.071	96.8 [1]	eastern	tagging	Victoria	(Sanders and Powell 1979)
-	0.068	111.9 [1]	western	tagging	Victoria	(Sanders and Powell 1979)
-	0.06	98.3	“Bay”	tagging	Port Phillip & Westernport Bays, Victoria	(Francis and Winstanley 1989)[2]
-	0.04	117.5	“Ocean”	tagging	Victoria	(Francis and Winstanley 1989)[2]
-1.11	0.102	58.8	SNA1	Otolith ages	Hauraki Gulf & Bay of Plenty, New Zealand	(Gilbert and Sullivan 1994) [3]
-1.40	0.128	46.2	SNA1	Otolith ages	East Northland, New Zealand	(Davies et al. 1999) [3]
-0.71	0.122	69.6	SNA7	Otolith ages	West Coast, South Island, New Zealand	NIWA (unpublished data) [3]
-0.11	0.160	66.7	SNA8	Otolith ages	West Coast, North Island, New Zealand	(Gilbert and Sullivan 1994) [3]
-2.86	0.194	90.19	NSG	Otolith ages	South Australia	This study

[1] total length

[2] re-analysis of (Sanders and Powell 1979)

[3] cited in (Annala et al. 2000)

Chapter 8. Population dynamics of *Pagrus auratus* in northern Spencer Gulf.

8.1 Introduction

The work described in the preceeding chapters has collected information and quantified key biological characteristics of *Pagrus auratus* such as growth, migration, age structure, relative yearclass strength and biomass. However, such biological data on fish populations is of limited value to fishery managers unless it can be translated into information that guides the decision making process (Schnute and Richards 1998). This can be viewed as a process of moving from a research emphasis on biological parameters to a management need for quantitative decision points, generally referred to as reference points. In turn, reference points can then be used to assess risks to the fishery (ie yields fall below sustainable levels) or to the stock (biomass falls below some minimum size) (Mace 1994). Historically, efforts were directed towards estimating reference points such as maximum sustainable yield (MSY) but the recent approach has been to develop a broader range of quantitative reference points (Caddy and Mahon 1995).

To derive reference points from the earlier results of this study, it is first necessary to integrate the biological information into a population model which describes the dynamics of *P. auratus* in northern Spencer Gulf. The output of the model can then be used to quantify the risk of defined events relevant to the future of the fishery. To this end, I have developed an age structured, dynamic model which incorporates the age structures, growth rates, migration rates and the biomass estimate of 1994 produced in this study, as well as fishery catch and effort data. The specific aims of the model were:

1) To integrate the biological and fishery data into a cohesive population model which estimates the trajectory of snapper biomass in northern Spencer Gulf over time,
2) To estimate the confidence limits for the biomass trajectory,
3) To predict the trend in biomass from 2000 into the future given the state of biological knowledge at that time, and

4) To assess the probabilities of future biomass performance against a number of biological reference points (BRPs).

8.2 Methods

8.2.1 Model overview

The snapper population was modeled using an age structured, single sex dynamic model which calculated numbers and biomass at age from 1983 to 2000. It was assumed that no stock recruitment relationship exists and annual recruitment for the 1979 to 1997 spawning years was estimated by the model. Numbers at age were calculated each year by applying migration rates, and fishing and natural mortality to estimates from the previous year. The models were fitted by maximum likelihood to combinations of catch at age proportions, catch per unit effort (CPUE) in the handline fishery and the 1994 estimate of spawning biomass. Model precision was assessed using a bootstrap procedure and the model was projected to 2020 using a range of assumptions from the initial model output.

8.2.2 Model parameters

The input data and parameters used for the modeling, bootstraps and projections are summarized in Table 8.1 and discussed in detail below.

8.2.2.1 Natural mortality

Natural mortality M was assumed to be independent of age and year and was set at 0.1. A wide range of values for M have been used for *P. auratus*, from 0.1 – 0.24 in South Australia (Jones et al. 1990; McGarvey and Jones 2000) and 0.04 – 0.08 in New Zealand (Annala and Sullivan 1997; Davies 1997). Age structured modeling of the West Coast New Zealand snapper stock population showed similar biomass trends within the tested range of 0.04 – 0.08 with compensation in recruitment estimates for increases in M (Davies 1997).

Table 8.1 Parameters used in the population model, bootstraps and model projections. Discussion of individual parameters follows.

Parameter	Model	Bootstraps	Projections
Natural mortality (M)	0.1 (9.5%)	0.1 (9.5%)	0.1 (9.5%)
Catchability (q)	5.004×10^{-5}	q +/- 2.14×10^{-5} (SD)	-
NSG fishing mortality (F_{NSG})	$q * E_t * V_{at}$	$q * E_t * V_{at}$	1) 0.125 +/- 0.022 (SD) 2) 0.1
Vulnerability (V_{at})	See Fig 8.1	See Fig 8.1	See Fig 8.1
Shelf fishing mortality (F_{shelf})	0.064	F_{shelf} +/- 0.023 (SD)	F_{shelf} +/- 0.023 (SD)
Residency (pNN)	59.5%	pNN +/- 14.3% (SD)	pNN +/- 14.3% (SD)
Emigration (pNO)	$1 - pNN - M$	$1 - pNN - M$	$1 - pNN - M$
Immigration (pON)	6.3%	pON +/- 2.99% (SD)	pON +/- 2.99% (SD)
Recruitment 1979 – 1997 (R_{79-97})	Estimated	Estimated	Resampled (R_{79-97})
Equilibrium recruitment (R_{70})	Mean (R_{79-97}) $= 4.99 \times 10^5$	4.99×10^5	-

8.2.2.2 Catchability, vulnerability and fishing mortality

The annual fishing mortality rate F_t was assumed to have a direct relationship with fishing effort and was calculated as $F_t = q*E_t$, where catchability q was estimated from the movement model as 5.004×10^{-5} (Table 5.5; 3 space model for all size fish). q was assumed to remain constant over the time period 1983 - 2000. Annual fishing effort E_t was a single standardized measure of effort and is discussed further in Section 8.2.3.1.

However, F_t was not applied uniformly with age due to differential vulnerability to fishing gears and because of the effect of a minimum legal length (LML). The data in the tagging analysis from which the catchability coefficient q was derived was based largely on fish < 5 years old (Chapter 6; Fig. 6.3). A few larger fish were also returned by longline fishers but their numbers were relatively small. It was assumed, therefore, that q was a reasonable estimation of catchability for age classes vulnerable to the handline fishery but underestimated catchability for age classes which were *also* vulnerable to the longline fishery. A vulnerability scalar $V_{g,a,t}$ was therefore calculated to produce an age and gear dependent $F_{g,a,t}$. It was assumed that the scalar = 1 for all age classes vulnerable only to the handline fishery and fully recruited to the fishery. From catch at age and growth results (Chapters 3, 7), this was assumed to be ages 5 –

12 (ie $V_{HL,\,5\text{-}12,\,t} = 1$). Catch at age showed that the presence of fish > 12 years decreased quickly to low proportions by the age of 15 (Chapter 3) and so $V_{HL,\,13\text{-}15,\,t}$ was incrementally reduced to 0.1 at 15 years and remained at that level until age 20+.

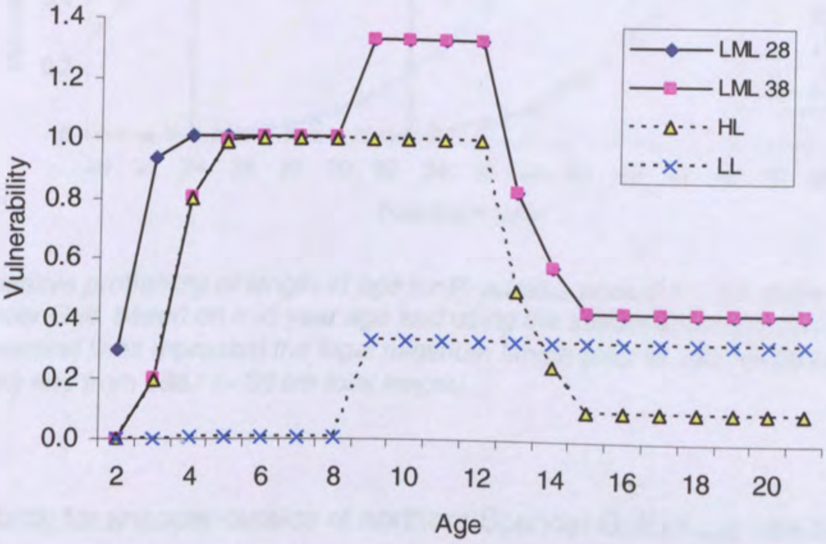


Fig. 8.1 Vulnerability curves for P.auratus in northern Spencer Gulf. The solid lines show total vulnerability at LML of 28 and 38 cm TL respectively. The dashed lines show the proportion of the handline (HL) and longline (LL) fishery to total vulnerability when LML = 38 cm.

For the longline fishery, catch at age has shown few fish at ages less than 9 and a high proportion of older fish up to maximum age. It was assumed that maximum vulnerability of fish to the longline fishery was equal to the average proportion of fishing effort that the longline fishery contributed to standardized effort ($V_{LL,\,9\text{-}20+,\,t} = 0.33$) (Fig. 8.1).

A proportion of fish were less than the LML at ages 2 – 4 years (Fig. 8.2). The vulnerability scalar was reduced to the proportion of fish that would have been greater than the LML midway through the year using the seasonal growth curve generated from otolith ages (Fig. 8.2). LML changed from 28 cm to 38 cm total length in 1987 and so the vulnerability scalar also had a time component (pre- and post-1987) at ages 2 – 4 (Fig 8.1).

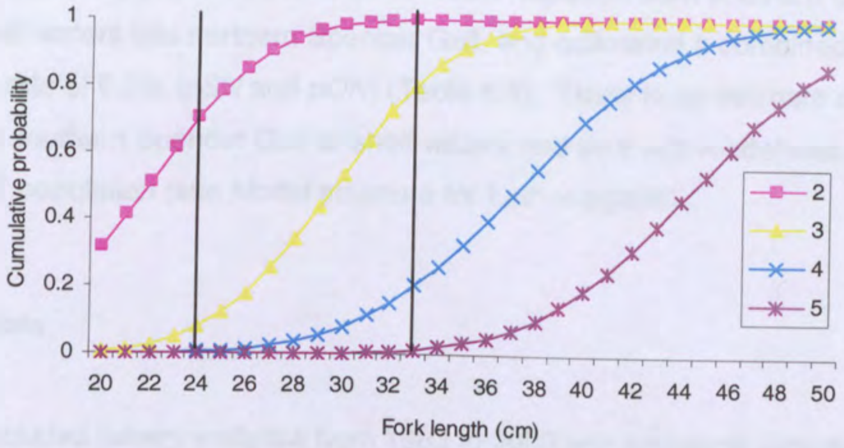


Fig. 8.2 Cumulative probability of length at age for P. auratus ages 2.5 – 5.5 years in northern Spencer Gulf, based on mid-year age and using the seasonal growth curve (Eq. 7.3). The vertical lines represent the legal minimum length prior to 1987 (≈ 28 cm total length) and from 1987 (≈ 38 cm total length).

Fishing mortality for snapper outside of northern Spencer Gulf (F_{shelf}) was calculated as the mean of the values of F_{shelf} from 1988 – 96 estimated in the movement model for shelf waters (Chapter 6).

8.2.2.3 Residency and emigration

The movement model of Chapter 6 estimated a residency rate (*pNN*) of 59.5% based on the number of snapper released and recaptured in Northern Spencer Gulf (Table 6.5; Model III). The movement model also estimated an emigration rate from NSG to the other defined spatial regions in the model, with the residual of the model being an estimate of movement to other (unspecified) regions after accounting for natural mortality. It was assumed, therefore ,that the best estimate of emigration from NSG was (1 – residency – natural mortality). The majority of snapper tagged were of lengths applicable to ages < 5 years. As no large snapper were recorded emigrating from NSG, it was assumed that emigration only applied to fish < 5 years of age.

8.2.2.4 Immigration

The tagging data also provided evidence of return migration from southern Spencer Gulf and shelf waters into northern Spencer Gulf, and estimated a combined immigration rate of 6.3% (*pSN* and *pON*) (Table 6.5). There is no estimate of biomass available for southern Spencer Gulf or shelf waters and so a sub-model was developed for the 'shelf' population (see Model structure for further details).

8.2.3 Input data

Input data included fishery statistics from 1983 to 2000 and biological data derived from earlier chapters and other sources.

8.2.3.1 Fishing effort

Estimation of fishing mortality rates required a single annual estimate of fishing effort from 1983 to 2000. A similar approach was taken to that used in the movement model analysis of Chapter 6, where effort of different sectors was standardized using CPUE of the commercial handline fishery as the basis for calculation, but was expanded to include the period 1983 - 2000 (Table 8.2). Recreational effort was assumed to remain constant over that time period and, while that assumption is unlikely to hold, its contribution to total standardized effort was only 9 – 15.5% (average 11.6%). CPUE of the handline fishery was also used as one of the criteria for model fitting.

Table 8.2 Input fishing effort and CPUE data used to estimate standardised effort from 1983 to 2000.

Year	Fishing effort (boatdays)					
	Commercial			Recreational	Standard	Handline CPUE
	Handline	Longline	Other			(kg.bday^{-1})
1983	1539	1088	90	319	3367	55.2
1984	1634	1048	90	319	3206	67.0
1985	1793	1058	35	319	2883	83.9
1986	1679	1247	40	319	3574	51.6
1987	1399	1110	47	319	3223	77.5
1988	1254	1047	74	319	2420	108.2
1989	1746	948	36	319	3091	94.1
1990	1563	823	45	319	2579	118.7

Table 8.2 (cont.)

Year	Fishing effort (boatdays) Commercial Handline	Longline	Other	Recreational	Standard	Handline CPUE ($kg.bday^{-1}$)
1991	1866	933	13	319	2738	97.2
1992	1880	933	76	319	3198	88.4
1993	1637	1220	29	319	2980	74.6
1994	1492	937	10	319	2605	63.0
1995	1606	950	2	319	2750	80.3
1996	1490	1133	1	319	2663	81.5
1997	1562	1123	0	319	2648	103.9
1998	1852	677	0	319	2411	127.9
1999	1713	560	0	319	2230	175.5
2000	1575	479	0	319	2058	155.2

8.2.3.2 Catch at age

Catch at age proportions were available for the handline fishery for three time periods – 1991 and 1994 from this study (Chapter 3) and 2000 (Fowler 2000) (Table 8.3). The proportions for 1991 and 1994 were reported with sampling error (cv; coefficient of variation) but none were available for the 2000 sample. Maunder and Starr (1998) reported a relationship between log transformed cv and log transformed proportion at age. A similar relationship was observed with the 1991 and 1994 samples ($\ln(cv) = -0.45 \ln(prop) - 4.66$; $R^2 = 0.75$) and this was used to generate cvs for the 2000 proportions.

Mean length at age was calculated from the seasonal growth curve generated from otolith samples. The cubic relationship $Wt\ (kg) = 1.56 \times 10^{-5} * LCF^{\wedge 3}\ (cm)$ has previously been used for South Australian snapper (Jones et al. 1990; McGarvey and Jones 2000). However, a new relationship of $Wt\ (kg) = 5.96 \times 10^{-5} * LCF^{\wedge 2.69}\ (cm)$ was developed for this study based on 529 fish measured and weighed (whole weight) during the DEPM surveys in 1994-6 (Fig. 8.3). Weight at age for 20+ fish was calculated from the length of a 25 year old fish.

Table 8.3 Catch at age proportions and coefficients of variation, and mean length and weight at age used as input data to the population model.

Age	1991 Prop	1991 cv	1994 Prop	1994 cv	2000 Prop	2000 cv	Mean length (cm LCF)	Mean weight (kg)
2	0.00	0.46	0.00	0.00	0.00	0.15	18.49	0.15
3	0.08	0.05	0.42	0.00	0.21	0.02	26.04	0.39
4	0.18	0.03	0.28	0.01	0.08	0.03	33.67	0.77
5	0.19	0.03	0.04	0.02	0.10	0.03	41.01	1.31
6	0.03	0.08	0.15	0.01	0.05	0.04	47.82	1.98
7	0.01	0.14	0.04	0.02	0.06	0.03	54.00	2.74
8	0.01	0.12	0.01	0.04	0.03	0.05	59.47	3.56
9	0.02	0.09	0.00	0.07	0.31	0.02	64.26	4.39
10	0.04	0.07	0.00	0.06	0.06	0.03	68.40	5.19
11	0.01	0.14	0.00	0.18	0.01	0.07	71.95	5.94
12	0.39	0.02	0.00	0.18	0.03	0.04	74.96	6.64
13	0.01	0.15	0.00	0.20	0.02	0.06	77.51	7.26
14	0.00	0.30	0.01	0.04	0.00	0.11	79.65	7.82
15	0.01	0.18	0.02	0.03	0.00	0.14	81.44	8.30
16	0.00	1.06	0.00	0.06	0.00	0.41	82.94	8.72
17	0.00	0.36	0.00	0.76	0.00	0.12	84.19	9.07
18	0.01	0.17	0.00	0.70	0.00	0.00	85.23	9.38
19	0.00	0.40	0.00	0.00	0.00	0.13	86.09	9.63
20	0.00	0.00	0.00	0.22	0.00	0.53	86.80	9.85
20+	0.01	0.13	0.01	0.00	0.02	0.05	88.89	10.50

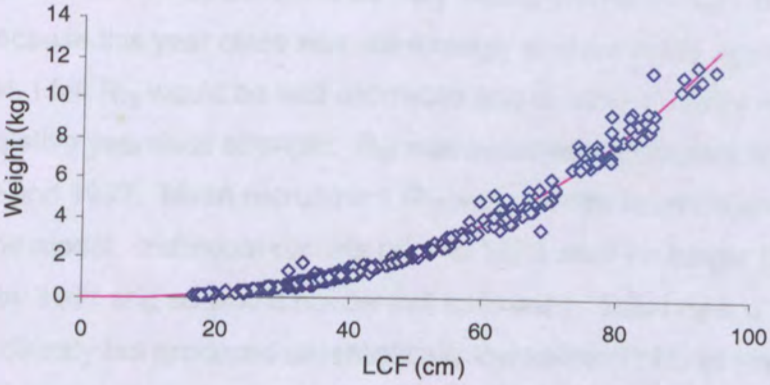


Fig. 8.3 Length weight relationship from 529 P.auratus collected from northern Spencer Gulf in November / December 1994, December 1995 and January 1996. The solid line represents the line of best fit Wt (kg) = $5.96 \times 10^{-5} * LCF^{\wedge 2.69}$ *(cm).*

8.2.4 Model structure

The base model was constructed in a series of yearly discrete steps from 1983 to 2000. Age classes from 2 - 20 were used as well as a single age class 20+ for the accumulated age classes > 20 years. Numbers at age *a+1* for year *t+1* were calculated by applying natural and fishing mortalities to numbers at age *a* for year *n* (Deriso et al. 1985).

$$N_{t+1,a+1} = N_{t,a}\, e^{-\sum_{g} F_{t,a} - M} \qquad (8.1)$$

Model catch at age for the handline fishery was calculated by

$$C_{ta} = \frac{F_{t,g,a}}{F_{t,g,a} + M}\left(1 - e^{-F_{t,g,a} - M}\right) N_{ta} \qquad (8.2)$$

The only parameters estimated were annual recruitment R_t, defined as the number of two year old snapper entering the fishery on January 1st in year *t*+2. Annual recruitment was therefore estimated for the spawning years 1981 to 1997. R_{98} was not estimated as they entered the fishery in the final year of the model and were not well represented due to very low vulnerability of 2 year olds. Three additional recruitments were estimated. These were R_{79}, R_{80} and mean recruitment prior to 1979, designated R_{70}. Recruitment in 1979 was shown to be very strong from the catch at age data in Chapter 3. Because this year class was still strongly present in the age structures in 1991 and 1994, I felt R_{79} would be well estimated and provide valuable information on the range of relative yearclass strength. R_{80} was included to complete the time series between 1979 and 1997. Mean recruitment R_{70} was needed to establish an initial age structure for the model. Individual cohorts prior to 1979 were no longer present in the age structure by 1991 and so would not be well estimated. Initial runs of the model estimated R_{70} directly but produced unrealistically low values (14% of mean recruitment $R_{79\text{-}97}$). Consequently, R_{70} was calculated as mean $R_{79\text{-}97}$ and allowed to vary with the iterations of the model.

One form of the model included return migration of snapper from southern Spencer Gulf and shelf waters to northern Spencer Gulf. As no biomass estimates were available for these populations, a "shelf" population was simulated from the emigrants from northern Spencer Gulf. It was assumed that the "shelf" population consisted only of the survivors of 2, 3 and 4 year old northern Spencer Gulf emigrants, and the numbers of which varied annually according to recruitment estimates for northern Spencer Gulf. Natural mortality was assumed to be the same as northern Spencer Gulf (= 0.1), and fishing mortality was assumed to be equal to the average F estimated for those waters in the movement model from 1988 to 1996 ($F_{shelf} = 0.064$).

8.2.4.1 Initial age structure

The number at age for 2 year olds was estimated directly by R_{81}. Numbers at age for cohorts 3 – 5 years in 1983 were estimated by subjecting the relevant recruitment estimate to emigration and natural mortality (calculated by applying the residency rate pNN) while fish older than 5 years were subject to annual fishing and natural mortality (Table 8.4). Fishing mortality prior to 1983 (F_{70}) was estimated as the mean of $F_{83\text{-}90}$ as fishing effort was not available for years prior to 1983. Fishing effort was scaled by the vulnerability scalar V_{at} for LML = 28 cm TL (Fig. 8.1).

Table 8.4 Derivation of initial numbers at age for 1983 biomass. The number of recruits (R_t) were reduced by the multiples of pNN, F and M indicated in the table.

Age group	Recruitment (R_t)	Residency rate (pNN)	Fishing mortality ($F\_70{*}V_{at}$)	Natural mortality (M)
2	R_{81}	0	0	0
3	R_{80}	pNN	$F\_70{*}V_{at}$	0
4	R_{79}	pNN^2	$(F\_70{*}V_{at})^2$	0
5	R_{70}	pNN^3	$(F\_70{*}V_{at})^3$	0
6-20	R_{70}	pNN^3	$(F\_70{*}V_{at})^{a-2}$	M^{a-5}

Where pNN = probability of fish tagged in NSG remaining resident in NSG (net of natural mortality and emigration)
F_{70} = fishing mortality pre-1983 (calculated as mean $F_{\text{NSG, 83-90}}$)
V_{at} = vulnerability at age a in year t
R_{70} = mean recruitment for years prior to spawning year 1979

8.2.5 Model fitting and sequence

A number of models were fitted to combinations of catch at age proportions, the 1994 biomass estimate and handline CPUE using maximum likelihood. The maximum likelihood estimators followed those used by Davies (1997) and Maunder and Starr (1998). Likelihoods were converted to negative log-likelihoods and minimized using the Solver routine in MS Excel.

8.2.5.1 Catch at age proportions

The likelihood function used to fit the model catch at age $\hat{P}_{y,a}$ to the observed catch at age was

$$L\left(P_{y,a}\right)=\frac{1}{\sqrt{2\pi}\,\sigma_{CA}\,cv_{a,t}}\,e^{\left(-\frac{\left(\ln\left(P_{a,t}\right)-\ln\left(\hat{P}_{a,t}\right)\right)^{2}}{2\left(\sigma_{CA\,cv_{a,t}}\right)^{2}}\right)} \tag{8.3}$$

where $P_{a,t}$ = proportion of the handline catch in numbers at age *a* in year *t*

$cv_{a,t}$ = the coefficient of variation of the catch at age *a* in year *t*

$\sigma_{a,t}$ = a variance scalar for the catch at age data

The variance scalar was used to scale the catch at age data relative to the CPUE data (Maunder and Starr 1998). The coefficient of variations of the observed catch at age account only for sampling error, are small and therefore heavily weight these age data. The scalar is calculated by

$$\sigma_{CA}=\sqrt{\frac{\sum_{a}\sum_{y}\frac{\left(\ln\left(P_{a,t}\right)-\ln\left(\hat{P}_{a,t}\right)\right)^{2}}{cv_{a,t}}}{n_{a}\,n_{t}}} \tag{8.4}$$

where n_a and n_t are the number of years with catch at age data and number of age classes respectively. The scalar was calculated when fitting the model to catch at age data only, and then fixed for models incorporating CPUE and biomass (Maunder and Starr 1998).

The negative log-likelihood for handline catch at age was therefore

$$-\ln\left(L(P)\right) = -\sum_{a}\sum_{t}\ln\left(L\left(P_{a,t}\right)\right) \tag{8.5}$$

8.2.5.2 Biomass

The likelihood function used for the spawning biomass estimate from December 1994 (designated B_{95}) was

$$L(B_{95}) = \frac{1}{\sqrt{2\pi}\,\sigma_B}\, e^{\left(-\frac{\left(\ln B_{95} - \ln \hat{B}_{95}\right)^2}{2\sigma_B^2}\right)} \tag{8.6}$$

where the model spawning biomass was calculated as the sum of all fish of ages >= 3 years and σ_B was the coefficient of variation of biomass bootstraps (= 0.21; Chapter 5).

8.2.5.3 CPUE handline

The likelihood function used to fit the time series of handline CPUE data was

$$L(CPUE_t) = \frac{1}{\sqrt{2\pi}\,\sigma_{CPUE}}\, e^{\left(-\frac{\left(\ln CPUE_t - \ln \hat{CPUE}_t\right)^2}{2\sigma_{CPUE}^2}\right)} \tag{8.7}$$

$CPUE_t$ (kg.boatday^{-1}) was obtained from the time series of fishery statistics (Table 8.2). The model $CPUE_t$ was calculated from the estimated model handline catch (Eq. 8.2) for ages 2 – 12 years for year t, divided by the handline effort for year t. The σ_{CPUE} was the cv of the CPUE indices.

The negative log-likelihood of the CPUE indices was therefore

$$-\ln(L(CPUE)) = -\sum_{t} \ln(L(CPUE_t)) \tag{8.8}$$

8.2.5.4 Model sequence

The model was first run by minimizing the catch at age likelihood function only. This provided a value for σ_{CA} for later models. While the catch at age model provided a good fit for catch at age proportions, other estimates (biomass and CPUE) were unrealistic and this model is not considered further. The model was then fitted in the following sequence;

1) catch at age and biomass (Model I)
2) catch at age, biomass and CPUE (Model II)
3) Model II plus immigration from shelf waters (Model III)

Immigration from the simulated “shelf” population to northern Spencer Gulf was tested by running Model III repeatedly using return immigration for all combinations of ages from 6 to 15. That is, return migration was simulated starting at age 6 and finishing at ages 6, 7, 8, ... 15. It was then tested again starting at age 7 and finishing at ages 7, 8, 9, ... 15, until all combinations had been tested. The log-likelihood of all combinations were then compared with the log-likelihood of the model without immigration.

The models estimated mean annual recruitment prior to 1979 (R_{70}) poorly. As a consequence, the biomass of snapper based on this recruitment was unrealistically low. This particularly affected the estimates of biomass of fish >15 years old prior to 1994 (when the strong 1979 yearclass entered this category). To provide a more reasonable estimate (so that spawning biomass trajectories over time became more meaningful), the final model with immigration was re-run using R_{70} as the mean of all other estimated recruitments $R_{79\text{-}97}$ rather than estimating it directly. R_{70} was then used as an equilibrium recruitment estimate for all years prior to 1979.

8.2.6 Model precision

The precision of Model III (fitted to catch at age, biomass and CPUE, and with immigration of 9 and 10 year olds) was assessed by a bootstrapping procedure using the parameter errors in Table 8.1. The error of fishing mortality for the NSG population was derived from the error of the catchability coefficient *q*, which was assumed to be lognormally distributed with standard deviation of 2.14×10^{-5} and was derived from the distribution of bootstrap estimates of *q* in the movement model analysis (Table 6.6). Fishing effort and vulnerability were assumed to be known without error. Fishing mortality for the shelf population was assumed to be normally distributed with standard deviation of 0.023, derived from the estimates of F_{shelf} from 1988 – 1996 in the movement analysis (Chapter 6). The errors for the rates of residency and immigration were taken from the bootstrap distributions in the movement analysis (Chapter 6) and were assumed to be normally distributed with CVs of 14.3% and 2.99% respectively.

The model was re-fitted 100 times using the resampled migration and fishing mortality rates and then re-estimated recruitment by minimizing the negative loglikelihood 100 times. The 90% confidence intervals of $R_{79\text{-}97}$, spawning biomass B_{sp}, biomass ages 3 – 15 $B_{3\text{-}15}$ and biomass ages > 15 $B_{>15}$ were taken from the bootstrap distributions and plotted against mean bootstrap estimates and the original model estimate.

8.2.7 Biomass projections to 2020 and performance indicators

The estimates of numbers at age for the year 2000 were used as an initial age structure to project the population to 2020. Shelf fishing mortality and migration (residency, emigration and immigration) rates were allowed to vary with the same error structures as those used in the bootstrap procedure (Table 8.1). Two alternative NSG fishing mortalities were used in the projections. The first was the average of $F_{NSG,\,t}$ from 1983 – 2000 ($F_{NSG,\,ave}$) as estimated annually in the model by the $q * E_t$ relationship. The annual $F_{NSG,\,t}$ ranged from 0.087 – 0.179, with mean of 0.125 +/- 0.022 SD (Table 8.1). The second was an estimate of $F_{0.1}$, which is a widely used reference point in fisheries management and is derived from the yield per recruit relationship. It is defined as the fishing mortality rate at which marginal yield is 10% of the marginal yield at the origin of the yield per recruit relationship (Hilborn and Walters 1992). $F_{0.1}$ was estimated at 0.1 from the yield per recruit data of McGarvey and Jones

(2000). Interestingly, $F_{NSG,\ ave}$ (0.125) appears to be close to F_{max} (fishing mortality that produces maximum yield per recruit) from the same yield per recruit analysis.

Annual recruitment for the years 2001 to 2020 was simulated by randomly resampling the recruitment estimates from the spawning years 1979 to 1997. In effect, this assumes that this distribution of recruitment estimates is representative of recruitment patterns over the next (or any) 19 year period. The projections were repeated 100 times for both $F_{NSG,\ ave}$ and $F_{0.1}$ with the other parameters resampled from their distributions.

A stepwise regression was used to determine the relative effect of four variables on the spawning biomass estimate for 2010 of each projection – 1) residency rate *pNN*, 2) immigration rate *pON*, 3) average recruitment over the 20 years $R_{ave\ 01\text{-}20}$ and 4) average fishing mortality over the 20 years (for projections using F_{ave}). The biomass estimates were lognormally distributed and were therefore log transformed before analysis. The proportion of total variation in the regression model was used as an indicator of the effect of each variable on future biomass estimates.

The biomass projections allowed an assessment of probabilities associated with the performance of the population and the fishery. Firstly a range of biomass, production and yield related biological reference points (BRP) were established (Table 8.5). Fisheries managers traditionally sought to harvest fish at a point near the estimated maximum sustainable yield (MSY), defined as the maximum yield on a curve describing the relationship between yield and fishing effort (Quinn and Deriso 1999). But experience and further theory development cast doubt on this interpretation of MSY as a safe target and a number of alternatives now exist (Caddy and Mahon 1995). These authors provide two interpretations of MSY for stocks subject to wide variations in recruitment. The first is a static interpretation of a constant yield considered to be sustainable at all future levels of biomass (maximum constant yield MCY). This necessarily implies a conservative approach to accommodate yields at low biomass levels. The second interpretation is a dynamic one where a constant instantaneous fishing mortality rate is applied to the predicted biomass in the year required to estimate a sustainable yield (current annual yield CAY). This method provides a yield which fluctuates with the level of biomass available and will, on average, provide a higher yield than a MCY approach.

Table 8.5 Biological reference points (BRP) used to assess future risk in the *P. auratus* fishery. Probabilities were calculated as the proportion of 100 biomass projections to 2020. See text for definitions of current surplus production (CSP) and current annual yield (CAY).

Biological reference point	Description	Method of calculation
P (CSP>CAY)>50% years	Probability that CSP exceeds CAY in 50 % of the projected years	Proportion of projections where CSP>CAY in at least 10 years
P (SumCSP>SumCAY)	Probability that total CSP over the 20 projected years exceeds total CAY	Proportion of projections where the sum of CSP exceeded sum of CAY
P ($B_{05,\,10,\,20}$>Bmid)	Probability that biomass estimates in 2005, 2010 or 2020 exceed Bmid where Bmid represents the mid point between the maximum and minimum model biomass estimates	Proportion of projections where the 2005, 2010 or 2020 biomass estimate exceeds 2,052t (B_{sp}), 1,708t ($B_{3\text{-}15}$) or 471t ($B_{>15}$)
P ($B_{05,\,10,\,20}$>Bmin)	Probability that biomass estimates in 2005, 2010 or 2020 exceed Bmin where Bmin represents the minimum model biomass estimates	Proportion of projections where the 2005, 2010 or 2020 biomass estimate exceeds 1,213 t (B_{sp}), 878t ($B_{3\text{-}15}$) or 359t ($B_{>15}$)

Because of the biomass fluctuations evident in the northern Spencer Gulf population, I have selected two BRPs associated with the dynamic yield CAY. The fishing strategy associated with a dynamic yield (ie. A constant harvest rate strategy) will exploit the population according to the available biomass, yielding higher catches in years of high biomass and lower catches in other years. In a population that exhibits fluctuations in biomass such as this one, a more conservative MCY fishing strategy would greatly under-exploit the population in years of high biomass but would also potentially increase the risk of stock collapse if a sequence of poor recruitment occurs (Sissenwine et al. 1988). The BRPs selected measure the relationship between CAY and the current surplus production (CSP), which was calculated as the increase in biomass from year *t* to *t+1* without fishing mortality (Davies 1997)

$$CSP_t = B_{t+1} + \sum_g \sum_a C_{t,g,a} - B_t \tag{8.9}$$

and model current annual yield (CAY) was calculated as

$$CAY = \frac{F_{ref}}{F_{ref} + M}\left(1 - e^{-(F_{ref}+M)}\right)B_t \tag{8.10}$$

(Annala et al. 2000)

Specifically, the two BRPs relating to CAY and CSP measured the probability that 1) CSP would exceed CAY in more than 50% of the 20 years of the projections to 2020 and 2) that the sum of CSP would exceed the sum of CAY over the same time period (Table 8.5). In both cases, these are essentially measures of whether the stock is likely to be increasing or decreasing in biomass. In these and other BRPs, probabilities were calculated as the proportion of the 100 projections which were conducted using the resampling techniques described above.

A number of additional biomass related BRPs were also used to test the probability that projected biomass will fall to two key levels - 1) Bmid, which was defined as the biomass midway between the maximum and minimum model biomass and 2) Bmin, defined as the minimum model biomass estimate. Bmid and Bmin were calculated from the full range of model estimates from 1983 to 2000 for B_{sp} and $B_{3\text{-}15}$ and from 1995 to 2000 for $B_{>15}$. The shorter time period was used for $B_{>15}$ as estimates prior to 1995 were based solely on cohorts generated from the equilibrium recruitment R_{70}. The catch history of this sector of the fishery shows that catches were high during the 1980s, increased further in the early 1990s and then decreased significantly through that decade to a low in 2000/01 (Fowler 2000). The biomass based on equilibrium recruitment therefore does not appear to properly reflect this pattern whereas model biomass trends do show a strong decline since 1995 to a low in 2000.

Bmin is considered a limit reference point (LRP) where drastic management action would be needed. Bmid on the other hand is seen as a level at which management interest should be aroused and particular attention paid to the direction in which biomass is trending. It may be used to trigger precautionary action if other indicators (eg age structure data) suggest a worsening situation. The use of biomass estimates from 1983 to 2000 as the basis for these BRPs assumes that the range of estimates reflects the full range of biomass variability in the population. There is some support for this given the range of commercial catches from record lows in 1994 to record highs in 2000 (handline fishery) and from record highs in 1997 to record lows in 2000 (longline fishery) (McGlennon & Jones 1997; Fowler 2000).

8.3 Results

8.3.1 Comparisons of models

The biomass estimates from the 3 models showed very similar trajectories with a decline to a low in the early 1990s followed by a sharp increase to 2000 (Fig. 8.4). There was very little difference between Models I and II (ie with the addition of CPUE in the likelihood function) but the addition of immigration in Model III increased biomass estimates by 20 – 25% after 1988 and improved the model fit over Model II. Model III was therefore adopted as the preferred model. The estimates of spawning biomass on January 1st 1995 exceeded the DEPM biomass estimate by approximately 20% in Models I and II and 26% in Model III (Fig. 8.4).

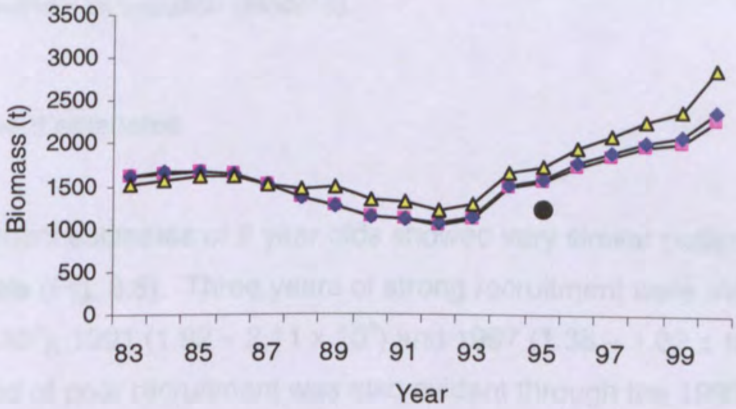


Fig. 8.4 Estimated spawning biomass of snapper aged 3 – 20+ years from 1983 - 2000. Models fitted to catch at age and biomass (□), catch at age, biomass and CPUE (◊) and the latter model with immigration added (Δ). The solid point represents the spawning biomass estimate from the daily egg production method survey in December 1994.

The negative log likelihood of Model III was minimized with immigration occurring at ages of 9 and 10 years but was less than Model II at all age combinations between 9 and 12 (Fig. 8.5). I interpret this to suggest that immigration generally occurs between those ages rather than restricted to 9 – 10 years.

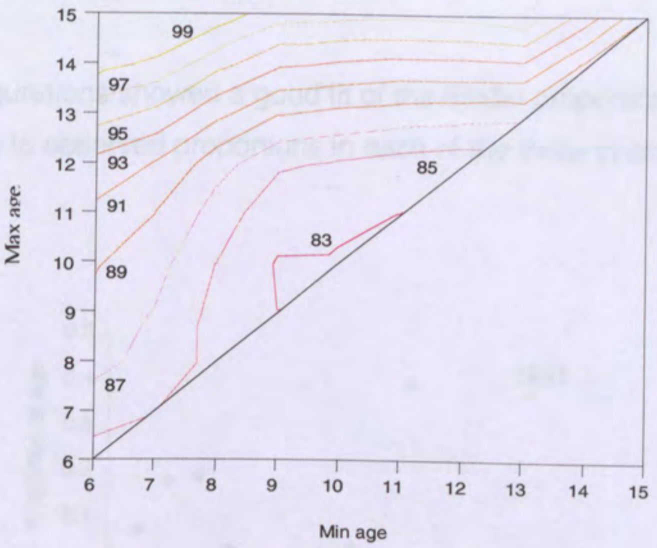


Fig. 8.5 Maximum likelihood contours for Model III with immigration age combinations between 6 and 15. The criterion of best fit used is a negative log likelihood and the best fit is therefore a minimum. The contour labeled 85 approximates the likelihood of the same model without immigration (Model II).

8.3.2 Recruitment estimates

Annual recruitment estimates of 2 year olds showed very similar patterns for each of the three models (Fig. 8.6). Three years of strong recruitment were evident - 1979 ($1.53 - 2.00 \times 10^6$), 1991 ($1.92 - 2.11 \times 10^6$) and 1997 ($1.35 - 1.62 \times 10^6$). An extended period of poor recruitment was also evident through the 1980s and, to a lesser degree in between 1991 and 1997. The average recruitment from 1983 to 1997 was 0.50×10^6.

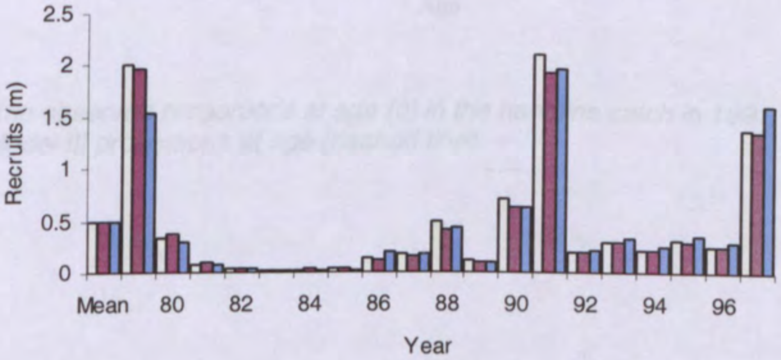


Fig. 8.6 Recruitment estimates (millions of 2 year old P.auratus) for Model I (yellow), Model II (red), and Model III (blue). Mean recruitment was used for all cohorts prior to spawning year 1979. Year denotes spawning year.

8.3.1 Catch at age

All model configurations showed a good fit of the model proportions at age for the handline fishery to observed proportions in each of the three years of catch at age data (Fig. 8.7).

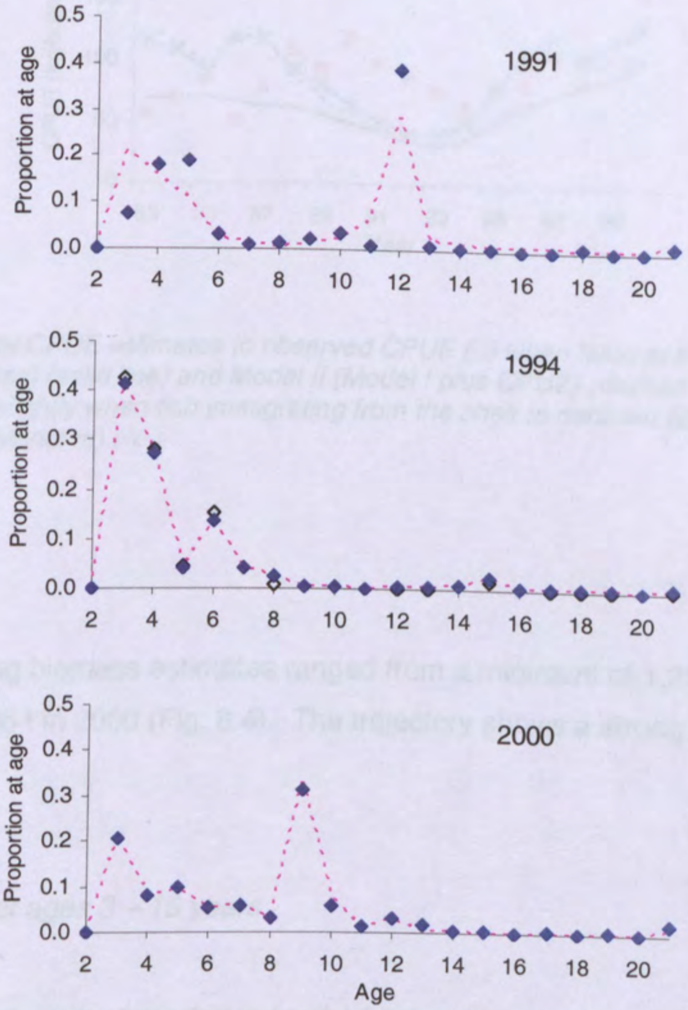


Fig. 8.7 Fit of the observed proportions at age (◊) in the handline catch in 1991, 1994 and 2000 with Model III proportions at age (dashed line).

8.3.2 CPUE

Model CPUE estimates underestimated observed CPUE when fitted to Model I (catch at age and biomass only) (Fig. 8.8). The addition of the CPUE likelihood function (Model II) improved the fit significantly although model CPUE estimates were still low at the higher of the observed values. These values occurred when the strong yearclasses of 1979 and 1991 were 11 and 8 years old respectively. The inclusion of fish immigrating from the shelf to northern Spencer Gulf further improved the fit, particularly in later years (Fig. 8.8).

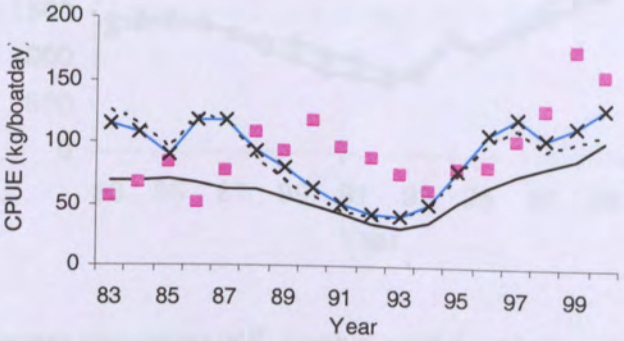


Fig. 8.8 Fit of model CPUE estimates to observed CPUE (□) when fitted to Model I (catch at age and biomass) (solid line) and Model II (Model I plus CPUE) (dashed line). The fit further improved slightly when fish immigrating from the shelf to northern Spencer Gulf were included (Model III) (-x-).

8.3.3 Biomass

Model III spawning biomass estimates ranged from a minimum of 1,213 t in 1992 to a maximum of 2,896 t in 2000 (Fig. 8.4). The trajectory shows a strong increase from 1992 to 2000.

8.3.3.1 Biomass of ages 3 – 15 years

All models showed similar trajectories for the biomass of ageclasses 3 – 15 years that are most vulnerable to the handline fishery (Fig. 8.9). Model III biomass decreased from levels of over 1,300 tonnes in the 1980s to a low of 878 tonnes in the 1992, and recovered to reach a peak of 2,537 tonnes in the latest year of the model in 2000. The rise in 1994 occurs due to the coincidence of the recruitment of the strong 1991 yearclass with the last year that the strong 1979 yearclass remains in this age grouping. The biomass of 3 – 15 year olds was typically 65 – 90% of spawning biomass.

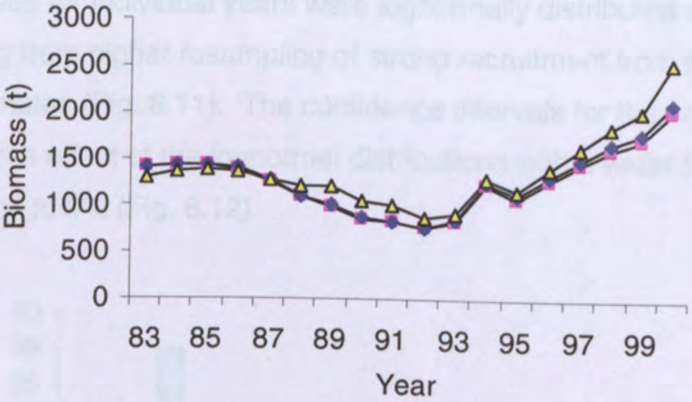


Fig. 8.9 Estimated biomass trajectories of P. auratus *aged 3 – 15 years for Model I (□), II (◇) and III (Δ).*

8.3.3.2 Biomass of ages > 15 years

The biomass of ageclasses of > 15 years before 1995 was made up of cohorts derived from the equilibrium recruitment prior to 1979. It therefore reflects an equilibrium population albeit subject to varying fishing mortalities during that period and is not necessarily a good reflection of real biomass fluctuations. In 1995, the strong 1979 yearclass moved into the > 15 year category causing a sudden increase in biomass (Fig. 8.10). The 1979 yearclass was followed by cohorts from very weak recruitments (see 8.3.2) and so biomass decreased quickly to a low of 359 tonnes in 2000.

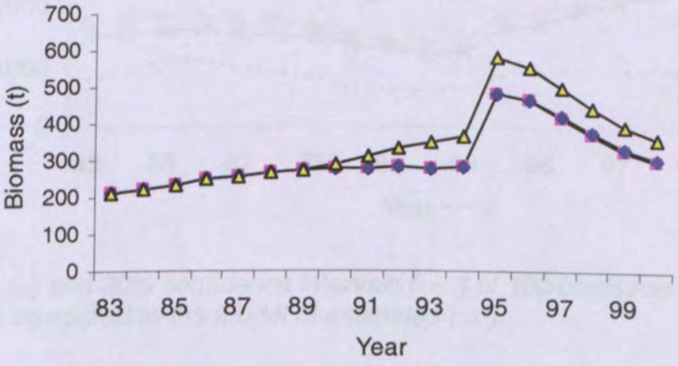


Fig. 8.10 Biomass of ages > 15 years. Models fitted to catch at age and biomass (□), catch at age, biomass and CPUE (◇) and the latter model with immigration added (Δ).

8.3.3.3 Precision of spawning biomass and recruitment estimates

Biomass estimates for individual years were lognormally distributed with extreme estimates arising from higher resampling of strong recruitment from the 1979 to 1997 recruitment estimates (Fig. 8.11). The confidence intervals for the spawning biomass trajectory show the effect of the lognormal distributions with a wider 95% confidence interval compared to 5% (Fig. 8.12).

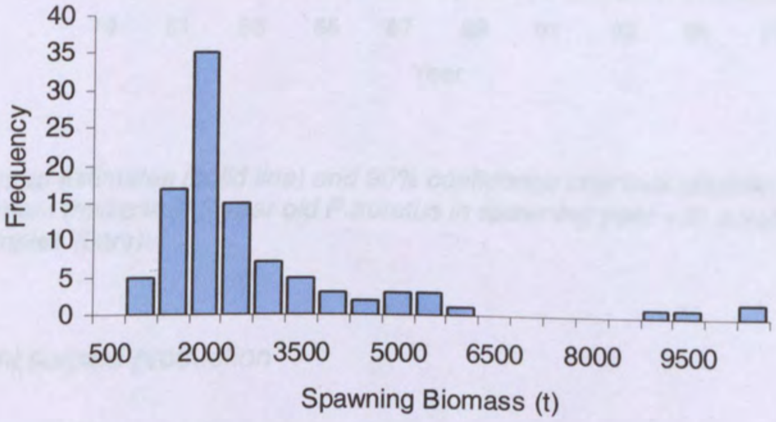


Fig. 8.11 Distribution of 100 spawning biomass estimates for 2020.

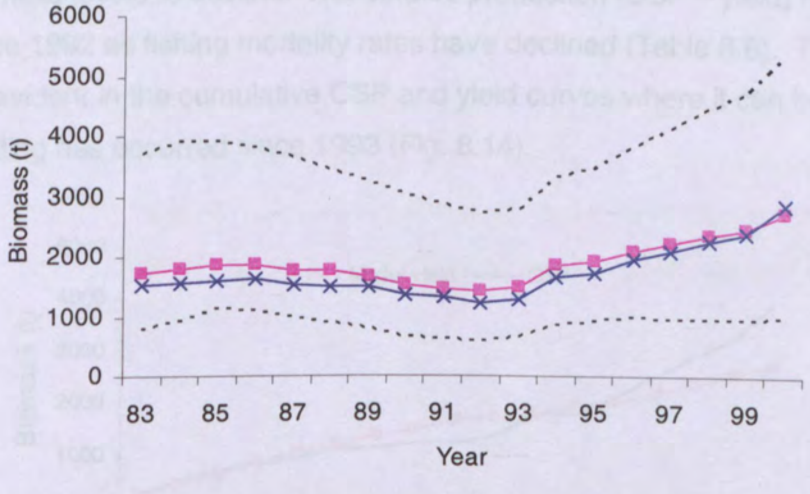


Fig. 8.12 Mean (--□--) and 90% confidence intervals (- - -) of 100 bootstrap estimates of spawning biomass compared to the Model III estimates (-x-).

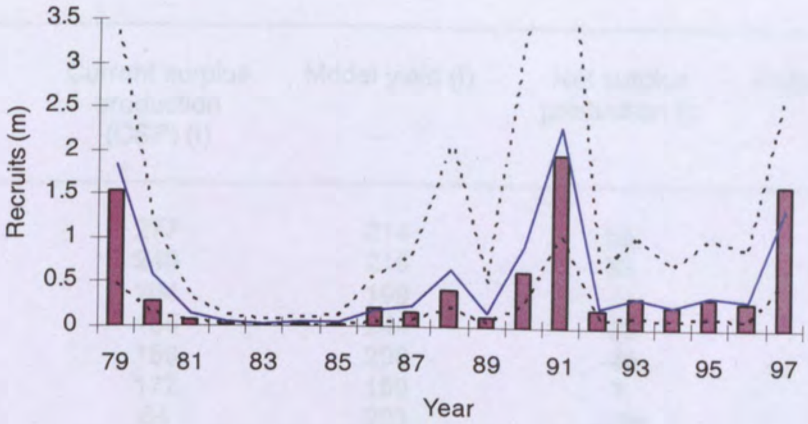


Fig. 8.13 Bootstrap estimates (solid line) and 90% confidence intervals (dashed lines) of recruitment (millions of 2 year old P.auratus in spawning year + 2) compared to Model III estimates (bars).

8.3.3.4 Current surplus production

Model current surplus production (CSP) declined during the late 1980s and early 1990s to a low of 40 tonnes in 1991 after which it has increased sharply to a high of 692 tonnes in 1999 (Table 8.6). Model yield exceeded CSP from 1986 to 1991 inclusive causing biomass levels to decline. Net surplus production (CSP – yield) has been positive since 1992 as fishing mortality rates have declined (Table 8.6). The pattern is particularly evident in the cumulative CSP and yield curves where it can be seen that stock rebuilding has occurred since 1993 (Fig. 8.14).

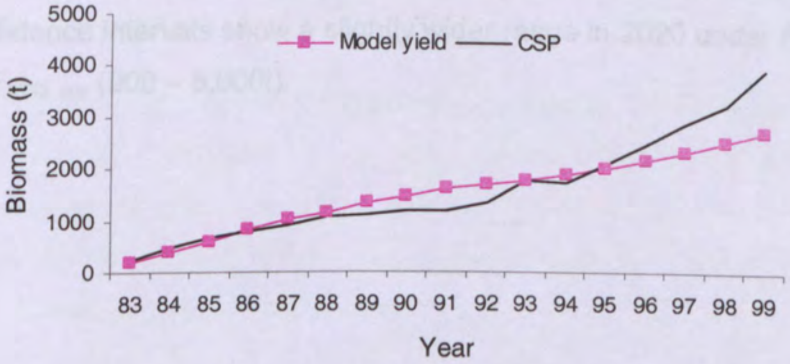


Fig. 8.14 Cumulative surplus production (CSP) and cumulative model yield from 1983 – 1999.

Table 8.6 Model III estimates of surplus production and yield compared to fishing mortality from 1983 to 2000.

Year	Current surplus production (CSP) (t)	Model yield (t)	Net surplus production (t)	Fishing mortality (*F*)
1983	277	214	63	0.168
1984	248	215	33	0.160
1985	204	199	5	0.144
1986	155	244	-89	0.179
1987	159	208	-49	0.161
1988	172	166	7	0.121
1989	64	203	-139	0.155
1990	115	147	-32	0.129
1991	40	138	-98	0.137
1992	194	127	68	0.160
1993	492	106	386	0.149
1994	186	107	79	0.130
1995	370	158	212	0.138
1996	351	192	159	0.133
1997	358	197	161	0.117
1998	322	196	126	0.105
1999	692	199	493	0.096
2000		225		0.087

8.3.3.5 Biomass projections 2001 – 2020

The mean spawning biomass projections to 2020 for the two reference fishing mortalities show different trajectories, with a 14% increase to 3,288 t under $F_{0.1}$ and an 8% decrease to 2,670 t under $F_{NSG,\,ave}$ from the starting estimate of 2,896 t (Fig. 8.15). The 90% confidence intervals show a slightly wider range in 2020 under $F_{0.1}$ (1,300 – 6,700t) than $F_{NSG,\,ave}$ (900 – 5,000t).

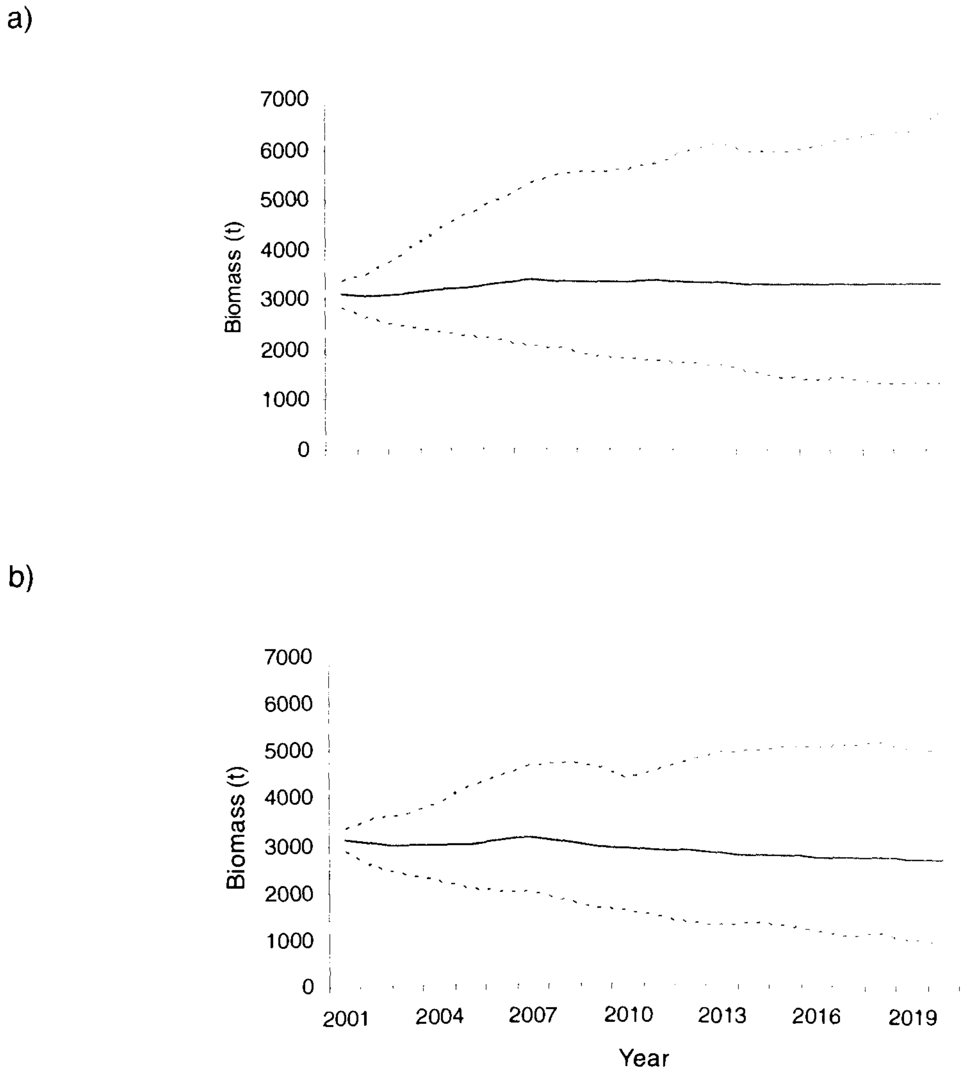


Fig. 8.15 Mean spawning biomass estimates (solid line) and 90% confidence intervals (dashed line) from 2001 to 2020 using reference fishing mortalities F_{ref} *of a)* $F_{0.1}$ *= 0.1 and b)* $F_{NSG,\ ave} = F_{max}$ *= 0.125*

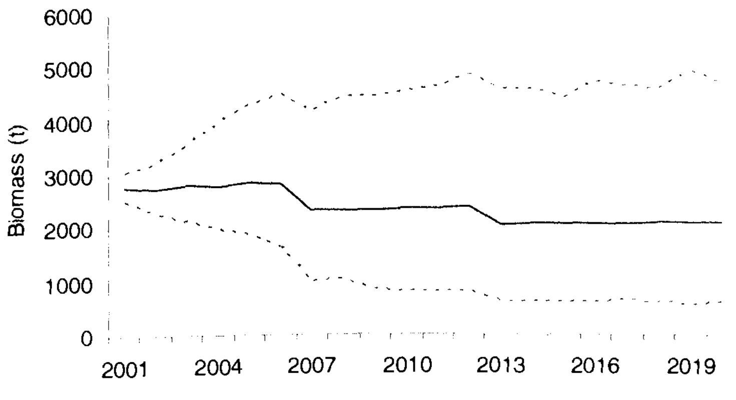
The contribution to the variance of a regression of spawning biomass estimates in 2020 (log transformed) projected under $F_{NSG,\ ave}$ was greatest for residency rates (*pNN*), followed by average recruitment over the 20 years and immigration rates (Table 8.7). The variation in fishing mortality (under $F_{NSG,\ ave}$) contributed little to regression variance although it remained statistically significant.

Table 8.7 Contribution to variance by four variables in a stepwise regression against spawning biomass estimates in 2020 (using the fishing mortality $F_{NSG,\ ave}$).

Step	Parameter	Sequential SS	R^2	Prob
1	Residency rate (*pNN*)	21.506	0.730	< 0.001
2	Average recruitment	4.500	0.883	< 0.001
3	Immigration rate	1.301	0.927	< 0.001
4	Average $F_{NSG,\ ave}$	0.324	0.938	< 0.001

Mean estimates of the biomass of ages 3 – 15 years showed declines of 16% ($F_{0.1}$) and 29% ($F_{NSG,\ ave}$) to 2020 (Fig. 8.16). Both trajectories show the loss of the strong 1991 and 1997 yearclasses in two steps in 2007 and 2013 respectively. The levels after 2013 reflect an equilibrium level based on average recruitment from the highly variable 1979 – 1997 recruitment estimates. The wide range of biomass estimates reflected in the 90% confidence intervals represent the effect that small increases (or decreases) in the number of strong yearclasses can have on biomass.

a)



b)

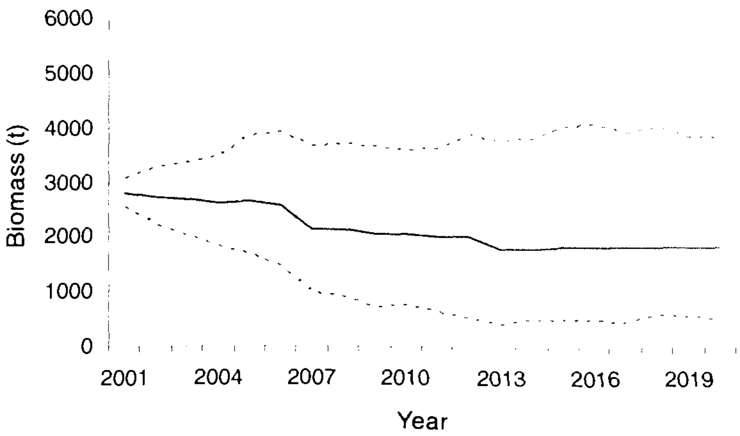


Fig. 8.16 Mean biomass estimates for ages 3 – 15 years (solid lines) and 90% confidence intervals (dashed lines) from 2001 to 2020 using reference fishing mortalities F_{ref} *of a)* $F_{0.1}$ *= 0.1 and b)* $F_{NSG, ave} = F_{max}$ *= 0.125.*

The patterns of biomass for ages > 15 years show the inverse trend to ages 3 – 15 years (Fig. 8.17). Two stepped increases occur in 2007 and 2013 as the 1991 and 1997 yearclasses join this age grouping. The low level of biomass prior to 2007 reflects the total dependence on the ageing 1979 yearclass with very little additional input from yearclasses until 1991. The addition of the two later strong yearclasses increased the biomass levels of fish > 15 years by 3-400% from 2000 levels.

a)

b)

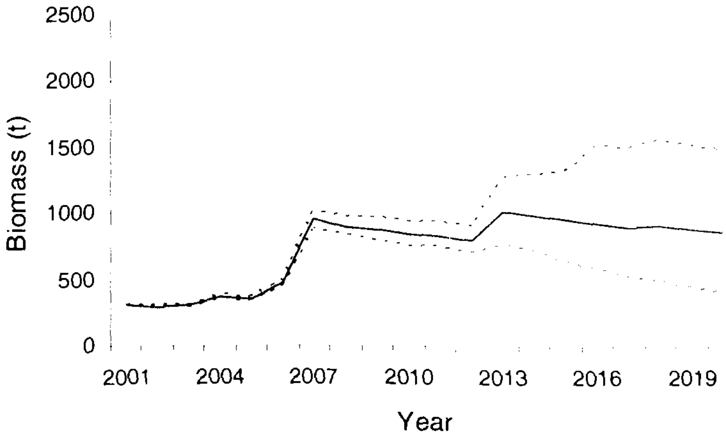


Fig. 8.17 Mean biomass estimates for ages > 15 years (solid lines) and 90% confidence intervals (dashed lines) from 2001 to 2020 using reference fishing mortalities F_{ref} of a) $F_{0.1} = 0.1$ and b) $F_{NSG,\ ave} = F_{max} = 0.125$.

8.3.3.6 BRPs

The probability that current surplus production of the 3 – 15 years group and of spawning biomass overall will exceed yield over the next 20 years is less than 50% with either a $F_{0.1}$ or $F_{NSG,\ ave}$ management strategy (Table 8.8). Both $B_{3\text{-}15}$ and B_{sp} were at record high levels in 2000 and it is therefore expected that they will decline. The biomass of fish > 15 years $B_{>15}$, however, was at record lows in 2000 and, with the addition of the strong 1991 and 1997 cohorts in 2006 and 2013 respectively, there is a 98 – 100% probability that cumulative CSP will exceed yield over the 20 year period (Table 8.8). This is predicted to occur despite a low probability that CSP will exceed annual yield in more than 50% of the years.

The probabilities of biomasses exceeding the key levels of Bmid and Bmin by 2005, 2010 and 2020 differed between $B_{3\text{-}15}$ and $B_{>15}$ (Table 8.8). Under the more conservative $F_{0.1}$ strategy, $B_{3\text{-}15}$ has more than an 86% chance of exceeding Bmin through to 2020 and 55% chance of exceeding Bmid. In both cases, the probabilities decline over time to those levels. In the short-term to 2005, $B_{>15}$ shows 100% probability of exceeding Bmin but 0% chance of exceeding Bmid. However, it is clearly in a stock rebuilding phase as it shows 99-100% chance of exceeding both levels in 2010 and 2020 (Table 8.8). As expected, the probabilities are slightly lower for the higher fishing mortality of an $F_{NSG,\ ave}$ management strategy.

Table 8.8 Probabilities associated with biological reference points (BRP) based on 100 population projections from 2001 to 2020.

	B_{sp}		$B_{3\text{-}15}$		$B_{>15}$	
Biological reference point	$F_{0.1}$	$F_{NSG,\ ave}$	$F_{0.1}$	$F_{NSG,\ ave}$	$F_{0.1}$	$F_{NSG,\ ave}$
P (CSP>Yield) > 50% years	38	21	25	11	15	0
P (SumCSP > SumYield)	42	24	26	18	100	98
P (B_{05} > Bmid)	97	93	97	92	0	0
P (B_{10} > Bmid)	90	78	68	57	100	100
P (B_{20} > Bmid)	75	60	55	45	99	89
P (B_{05} > Bmin)	100	100	100	100	100	14
P (B_{10} > Bmin)	100	99	93	90	100	100
P (B_{20} > Bmin)	96	85	86	75	100	98

The predictions for overall spawning biomass are determined largely by $B_{3\text{-}15}$. There are high probabilities (>85%) of exceeding Bmin to 2020 and > 60% of exceeding Bmid with either $F_{0.1}$ or $F_{NSG,\ ave}$.

8.4 Discussion

8.4.1 Model output

The age structured model has provided a coherent depiction of the changes in snapper biomass in northern Spencer Gulf from 1983 to 2000. The biomass trajectories were similar with each of the three Models and reflected the changes in commercial catches. The models all estimated a higher spawning biomass in January 1995 than the December 1994 DEPM estimate, and were greater than the 97.5% confidence intervals of the bootstrap distribution of that latter estimate. However, the DEPM estimate was limited to a sub-region of the study area and a higher model estimate was therefore consistent with expectations.

Differences between Models were evident in their fit to CPUE of the handline fishery (Fig. 8.8). The best fit occurred with Model III that included an immigration component of 9 and 10 year olds. Model CPUE over-estimated observed CPUE for the period prior to 1987 which may further indicate a poor estimate of recruitment pre-a979. But model CPUE underestimated observed CPUE during the periods of highest catch rates (1990-3 and 1998-00). There are a number of reasons that this may have occurred. Firstly, the highest catch rates occurred when the strong yearclasses of 1979 and 1991 were 11 – 14 years and 7 – 9 years respectively. The age structures of 1991 (this study) and 2000 (Fowler 2000) show that these strong yearclasses were largely responsible for the high catches. The model has incorporated a return immigration from the shelf based on a hypothetical shelf population derived entirely from NSG emigrants. It is possible that this method of generating the population underestimates its size and/or the rate of immigration (6.3%) underestimates their return. It is acknowledged that this rate was estimated from a tagging dataset that was limited for tag releases outside of NSG.

Another potential reason for the relatively poor CPUE fit may be that the vulnerability schedule for fish aged (say) 7 – 14 years may underestimate their vulnerability to fishing at those ages. Vulnerability was derived from an interpretation of age and gear specific catches and further work may be warranted to better define this parameter. Alternatively, vulnerability could be estimated by a more complex version of the model, adding a x g (= 20 years x 2 geartypes) parameters (Deriso et al. 1985).

The spawning biomass trajectory was largely determined by the biomass of cohorts aged 3 – 15 years, which contributed 65 – 90% of spawning biomass. The trajectory showed a decline through the late 1980s and early 1990s to a low in 1992, followed by strong growth to 2000. This pattern was generally reflected in the pattern of handline catches, with record lows in 1994 followed by increases to a record high in 2000. The biomass of the fish > 15 years was not well estimated prior to 1995 due to its dependence on the mean recruitment parameter. Superimposing commercial longline catches on this biomass trajectory shows that it is likely that (a) strong yearclass(es) occurred in the late 1960s or early 1970s to contribute to higher biomass from 1983 to 1987 than the model predicts (Fig. 8.18). The age structure of the longline fishery in 1994 showed a potentially strong yearclass from 1973 (Fig. 3.16). The trajectory from 1995 to 2000 represents the almost sole contribution of the 1979 cohort with little additional biomass from subsequent years.

Fig. 8.18 Model III biomass snapper > 15 years (-△-) compared to catches in the commercial longline fishery (----) 1983 – 2000.

It should be noted that this geartype does not exclusively target fish > 15 years old, with the strong 1979 and 1991 yearclasses evident as 12 and 9 year olds respectively (Fig. 3.16; Fowler 2000). This may explain the peak in catches in 1992 and 1993 not predicted by > 15 years biomass patterns. It is also evident from more recent age sampling that this sector is capable of targeting even small snapper with the 1997 cohort well represented in 2000 – 2002 age structures (Fowler et al. 2003).

8.4.2 Projections, BRPs and outlook for the stock

The biomass projections make a number of assumptions regarding the fishery and the snapper population. Significantly, they assume that the frequency of strong yearclasses from 1979 to 1997 (ie 3 strong years mixed with 16 relatively poor years) is representative of the distribution of future yearclass strength. This pattern appears to have continued for at least the next 5 years, with juvenile trawl surveys suggesting that 1998, 2000, 2001 and 2002 are unlikely to be strong yearclasses although 1999 shows some potential (Fowler et al. 2003). The strength of that yearclass will be better understood as it fully recruits to the fishery. The model has assumed no stock recruitment relationship and, certainly within the range of biomass estimated from 1983 to 2000, this appears to be true. In fact it should be noted that the strongest yearclass in 1991 was produced when spawning biomass was near its lowest levels. Similar assumptions are held true for the West Coast New Zealand snapper population

(Davies 1997) and for Hauraki Gulf where recruitment strength is believed to be related to water temperature (Francis 1993; Maunder and Starr 1993).

Biomass projections were most affected by the residency rate used, which determined the rate of emigration from NSG. Emigration was assumed to occur at ages 2 - 4 only and to be constant within those ages. The rate was allowed to vary with each projection according to the bootstrap distribution of *pNN* established in the movement model of Chapter 5, and ranged from 0.185 – 0.881. Further work on the variability of emigration rates (both in terms of inter-annual and age dependent variability) will allow better estimation of future biomass. Analysis of the otolith microchemistry of snapper is now being used as a tool to further investigate migration patterns in South Australia (Dr T Fowler, pers. comm.).

The biomass projections provide a level of confidence for the status of the northern Spencer Gulf stock even though there is > 50% and > 80% probability that B_{sp} and $B_{3\text{-}15}$ will decline over the years to 2020. Both B_{sp} and $B_{3\text{-}15}$ were at high levels in 2000 and there remains a 78% and 57% probability respectively that they will be above the 1983 – 2000 mid level in 2010 even if fishing mortality continues at $F_{NSG,\,ave}$ (= 0.125). Even by 2020, the probabilities are 60% and 45% respectively and a more conservative $F_{0.1}$ approach increases those probabilities by 10 – 15%. Monitoring of future recruitment strengths by trawl surveys and age structure analysis will allow relatively simple means to improve the confidence of these predictions.

On the other hand, there is almost 100% probability that biomass of fish > 15 years will increase as the 1991 and 1997 yearclasses recruit to this category (assuming no substantial changes in fishing mortality as they pass through the handline fishery). This will allow for rebuilding of this portion of the spawning population as a hedge against a series of future recruitment years. It can therefore be concluded that the strong 1991 and 1997 yearclasses have strongly reversed the declines apparent in the 1980s and early 1990s and leave the stock in a strong position.

Chapter 9. General discussion and conclusions

The study of the fisheries biology and population dynamics of snapper *Pagrus auratus* described in this thesis had two broad objectives:

1) To gain a better understanding of the life history of the species and to determine whether there was a biological cause for both the decline in the commercial catches and the cycles evident in them and,
2) To integrate biological and fishery information into a simple population model which provided a coherent depiction of the dynamics of the snapper population and which could be used to provide guidance to fishery management decisions.

This concluding Chapter summarises the key outcomes of the study, offers some general conclusions and suggests some directions forward.

9.1 Key outcomes of the study

The outcomes are structured according to the Chapters in the thesis.

9.1.1 Age composition of the commercial catch

The study of the age composition of the commercial catch sought to identify whether inter-annual recruitment variability was a possible cause of the fluctuations and significant decline in commercial catches in the early 1990s. Two key outcomes were achieved; the establishment of a robust ageing process, and evidence of highly variable recruitment.

The ageing process based on the interpretation of otolith annuli was shown to be robust, with good precision and low bias. The process has provided a cost-effective method of snapper ageing and has formed the basis of regular age composition analysis in recent years (Fowler 2000; Fowler 2002; Fowler et al. 2003). The reliability of the ageing process is evident from the consistent identification of strong yearclasses through the sampling years of 1991 – 2002 in those reports.

The strong evidence for highly variable recruitment has been a significant advance in our understanding of the population biology of *P.auratus* in South Australia. The previous understanding based on ageing from scale readings had assumed there was not variable recruitment and that fluctuations in catches and assumed biomass were largely due to the effects of fishing. It is now apparent that the environmental forces that result in highly variable recruitment have far more influence than fishing activity. The age composition of the commercial catch is now routinely studied as part of the snapper research program, and has been extended to include Southern Spencer Gulf and Gulf St Vincent. These studies have shown significant consistency in yearclass strengths across regions which suggests that the processes which are driving recruitment variability are acting on a regional scale.

The strong influence of environment relative to the activities of the fishery does not diminish the need for careful fishery management. It is vital that each individual strong yearclass is not fished down to the extent that its contribution to spawning potential is lost in the absence of subsequent strong yearclasses.

Another significant outcome of this study was an understanding of the differences in gear-type specific age compositions, which provided evidence of the different age classes targeted by the handline and longline sectors. This has provided an insight into the relative effect that each sector has on the population and assists in resource sharing issues in management of the fishery. There is some evidence that the age classes targeted by the longline sector have broadened in recent years due to the relative scarcity of the older yearclasses (Fowler et al. 2003). Continued monitoring of the age compositions of each sector will allow an assessment of the effects on overall exploitation rate of such a trend.

I believe that continuing data collection on the age structure of snapper provides more valuable information to the fisheries management of the species than any other single study. It allows a coherent interpretation of fluctuations in catches, both gear specific and overall, and provides a means to forecast population trends some years in advance.

Of course, age composition provides only a snapshot of the results of a number of ecological and biological processes which have resulted in recruitment variability. It does not provide any information on the causative processes which have given rise to such results. It is of significant ecological (if not necessarily fisheries management) interest to understand the processes producing this result. The research programme has more recently directly investigated the spatial distribution of 0+ snapper in NSG in an effort to direct more research effort towards such an understanding (Fowler 2000).

9.1.2 Reproductive biology and DEPM biomass estimates (Chapter 5)

The primary aim of the DEPM study was to provide an independent estimate of spawning biomass. However, the study also provided some new biological information on the reproductive biology of *P.auratus*:

a) plankton sampling for the DEPM provided the first spatial patterns for spawning in South Australian waters
b) ovary sampling provided the first estimates of batch fecundity for South Australia
c) adult fish sampling allowed development of a new length weight relationship
d) the study also developed the relationship between temperature and egg development.

The density of eggs was generally low and spatial patterns of spawning between months and years was not consistent enough to determine discrete spawning areas. However, egg densities and the proportion of spawning females in the adult fish samples suggested that more spawning activity occurred in the central part of the study area, and possibly more so on the western coast. A later study found little similarity in egg distribution apart from an area of concentrated abundance near the entrance to Franklin Harbor near Cowell (Fowler 2002). While these separate studies have not isolated clear spawning areas, it would appear that the western coast of the Gulf from an area south of Whyalla near Murninnie to the entrance to Franklin Harbor, and east to the central Gulf near Middle Bank, offers the most potential for further study of spawning.

Other outcomes of the study related to spawning and early life history included estimates of batch fecundity, time of day of spawning, sex ratio, size at first maturity and spawning frequency (all Chapter 5), as well as an understanding of the effect of temperature and salinity on the development of eggs and larvae (Chapter 4). These not only provide a better understanding of the biology of *P. auratus* in Spencer Gulf but also provide estimates of parameters of direct interest to fisheries managers (e.g. size at first maturity).

Of four attempts to estimate biomass using DEPM, only the December 1994 estimate could be used with confidence, and this estimate was restricted to a sub-region of the study area. The critical limitation in the future use of the DEPM is the inability to representatively and independently sample adult fish throughout the study area. There are clearly spatial differences in spawning activity and the reliance on commercial fishers to provide samples does not allow for adequate stratification of the area.

Despite the limitations of the method for the population in this area, the December 1994 estimate of biomass did provide a useful scalar for the annual biomass estimates by the population model of Chapter 8. Initial estimates fitted to catch at age proportions and CPUE yielded implausible biomasses exceeding 5,000 tonnes. Inclusion of the DEPM biomass estimate to the fitting procedure scaled the estimates to more realistic levels ranging from 1,500 – 3,000 tonnes. The model estimated spawning biomass of 1,745 tonnes in January 1995 which exceeded the DEPM estimate by approximately 32%. But, as the DEPM estimate applied to a spatially restricted region of the study area, this was a plausible outcome.

I would not advocate further research effort be applied to refining the DEPM for Northern Spencer Gulf because of the difficulties in providing spatially representative sampling of the adult fish. And a study limited to the central part of Northern Spencer Gulf, which potentially could be sampled adequately in times of high abundance, would only be of value to management of the species if it was conducted regularly to establish a time series of relative estimates of biomass.

9.1.3 Migration

The analysis of the tag recapture data quantified movement rates in Spencer Gulf and beyond for the first time. Such an outcome allowed explicit movements to be expressed in the model of the NSG population. The movement model was used both on the full tag recapture data-set and on sub-sets (size and spatial). The models yielded similar residency rates for NSG (57 – 59%) and for SSG (62 – 67%) for each of the data-sets used. The relatively high residency rates were expected given the high proportion of fish which were recaptured at or near their site of release.

The rate of movement between Spencer Gulf and the shelf outside of the Gulf were probably underestimated. The residuals of the movement probabilities were generally more than 30% and a large part of this could be explained by movement into areas not adequately covered by fishing effort, and therefore tag recapture. This "poor" coverage of fishing effort on the shelf remains an impediment to the value of future tagging programmes for this species, in particular those which use passive tags that depend on the recapture of the individual tagged fish to yield information. Of far more potential is the use of archival tags, particularly those with sacrificial links which release the tag at a given time and allow the transfer of data via satellite. This method removes the need to recapture the tagged fish. At this time, the size and price of these tags is prohibitive for *P. auratus* but future developments may allow their cost-effective use.

The use of indirect methods such as the analysis of otolith microchemistry patterns to infer movement patterns also offers great potential. A study is currently underway to investigate the use of this technique for this purpose (T. Fowler, pers. comm.). This technique also has the potential to provide evidence on the level of mixing between Gulf St Vincent and Spencer Gulf, an issue that is of great interest given the significant and long-term decline in the snapper population of the former area.

In conclusion, I would not advocate further passive tagging of *P.auratus* in South Australia. I believe the value of this technique in describing movement and growth (see next section on Growth) has been exhausted unless reliable access to shelf populations became possible, and even this would require access to fish in shallow water where the effects of barotrauma during capture could be limited.

9.1.4 Growth

The estimation of growth rates used all available data from the tagging programme and the age length keys developed during this study. The study found evidence that growth was affected by tags, in particular loop tags, and found that growth rates estimated from tag recapture data were around 10 – 15% lower than those estimated from the age length keys.

Growth estimated from ages based on otolith readings showed a higher rate of growth to the asymptotic length than other published studies for *P. auratus*, but was accompanied by high rates of variability between individual fish. This variability explains the large range of lengths at age and the consequent difficulty in detecting yearclasses before the otolith ageing process was developed. The study also provided the first evidence for strong seasonality in growth.

9.1.5 Population dynamics

The objectives of the study were to better understand the fisheries biology and population dynamics of *Pagrus auratus* in northern Spencer Gulf in an effort to understand the significant variations in commercial catches, and the resultant concerns about the sustainability of current fishing practices. Each element of the study has contributed to this understanding and has allowed the development of a model which not only helps explain past events but provides management guidance for the future.

The population model integrates the outcomes of the previous chapters into a tool which can be used to support management decisions i.e. to translate biological data into information which guides the management process (Schnute and Richards 1998). The key inputs of age composition, growth, migration and biomass generated in this study were combined with fishery statistics to produce a biomass trajectory from 1983 – 2000, and then to make projections to the year 2020. Bootstrap iterations of the model projections were then used to determine the probability of exceeding a number of defined biological reference points (BRPs).

It is clear that the overall patterns in biomass over time are determined by highly variable inter-annual recruitment and the age composition that results. The sharp decline in catches in the early 1990s was largely a result of the long series of weak yearclasses in the 1980s. The very strong yearclass of 1991 then caused a rise to record catches in the late 1990s. Such an influence by a single yearclass is a feature of this population and fishery.

The model projections to 2020 were based on a distribution of yearclass strengths which is similar to that of the 20 years prior to 2000. Should that assumption hold true, there is a high level of confidence that the fishery will be sustainable. The research effort needed to monitor yearclass strength via analysis of age composition is relatively straightforward, and has been adopted as an annual project (T. Fowler, pers. comm.). It therefore becomes feasible to update the biomass projections and BRP probabilities and maintain a long term outlook for the fishery, something which is not commonly available with any confidence.

The model was constructed using a number of simplifications and assumptions. These included:

- an assumed vulnerability by age and gear schedule,
- an assumption that fishing mortality was directly related to fishing effort by a catchability coefficient which was fixed over time,
- an assumption that fishing effort could be standardized between gear-types by a simple ratio of CPUE,
- the construction of a "shelf" population which was derived solely from NSG emigrants and which solely supplied immigrants back to NSG, and
- a constant recreational harvest over time.

There is no doubt that some of these assumptions could be tested and a more complex model developed. Further, the assumption about the recreational harvest is undoubtedly an over-simplification – a recent study of recreational fishing has estimated a recreational harvest of approximately 370 tonnes (Henry and Lyle 2003), which is >400% higher than previous estimates (McGlennon and Kinloch 1997). But, for the purposes of this study, the model has satisfied its objective of integrating the biological and fishery data into a meaningful management tool. The results show good similarity to those reported from a more complex model developed by Dr Rick McGarvey (Fowler et al. 2003). For example, the estimate of biomass for NSG for year 2000 was approximately 3,000 t (Fig. 61; Fowler et al. 2003) compared to 2,896 t in this study.

9.1.6 Future research directions

The study of *P. auratus* in northern Spencer Gulf has provided new information on a number of aspects of the fisheries biology of the species and integrated them into a population model which is both simple and coherent. It is feasible that fisheries management would require no more than a regular determination of age composition study and an update to the population model based on the new data. The age compositions would not even be needed annually, given the longevity of the species and the extended time that each yearclass is fished. I could envisage a timeframe of every 3-4 years being adequate if resources were limited.

The other outstanding issue of importance to fisheries managers is the movement patterns between Spencer Gulf, Gulf St Vincent and the shelf. This is particularly so in terms of an understanding of the dynamics of the Gulf St Vincent population, but also in terms of the role and extent of the exchange between the shelf and NSG. The current study of otolith microchemistry may provide an insight into these movements.

In addition to issues of fisheries management significance, there are a number of aspects of snapper biology which are of more general biological and ecological interest. Little is known of the early life history of the species in South Australia. A series of trawl surveys of 0+ - 2+ snapper in NSG have been conducted as an initial step in investigating the spatial distribution of juveniles (Fowler et al. 2003). The cause of the extremes in recruitment variability is of significant interest and these surveys may provide the basis of designing a targeted study of the influences on juvenile snapper.

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