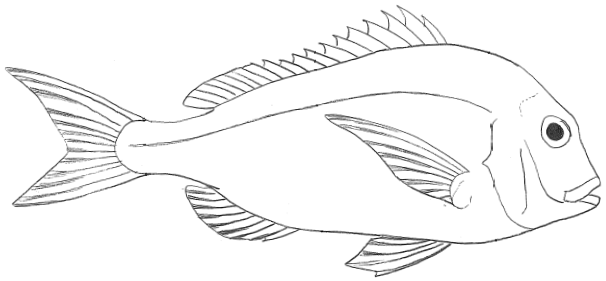
The reproductive biology and recruitment dynamics of snapper, *Chrysophrys auratus*



Richard J. Saunders

School of Earth and Environmental Sciences
University of Adelaide

Thesis submitted for the degree of Doctor of Philosophy

July 2009

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Declaration

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Acknowledgements

This research was supported by a University of Adelaide Divisional Scholarship with the School of Earth and Environmental Sciences and discretionary funds from the Marine Scalefish Fishery Management Committee to SARDI Aquatic Sciences.

Thanks must be extended to my academic supervisors Dr Anthony Fowler and Associate Professor Bronwyn Gillanders who have offered unfailing support throughout the whole process and did not despair, even when reading early drafts.

Don Dew provided space at the SAFCOL Fish Market (in the fridge) where the samples of adult snapper were dissected! Without this space and access to fish, allowed by innumerable fish processors, retailers and wholesalers, the reproductive biology data set would not have been able to be collected. Charter fishermen Trevor Bennett and Garry Barnes both provided samples on several occasions.

Staff from the South Australian Aquatic Sciences Centre including Bruce Jackson, Matt Lloyd, Mike Steer, David Fleer, Graham Hooper, Paul Van Ruth and Bruce Miller-Smith assisted in the field and/or in the fridge at SAFCOL on many occasions. In particular, Bruce Jackson and Matt Lloyd laboured through the dead of night in northern Spencer Gulf operating an inconceivably recalcitrant beam trawl net with an exceptionally unreliable winch in persistent south-easterly gales.

The crew of the RV Ngerin, Neil “Chicko” Chigwidden, Dave Kerr, Ralf Putz and Chris Small, have run the otter trawling for the past nine years, sorted catch and mended the net. Their experience and skills have been invaluable in the planning and execution of the sampling used throughout this research.

Paul Hamer was a great help in the early stages of the process by assisting with the development of the beam-trawl survey, providing insight into the methods he used in Victoria and sending me a spare beam trawl net to use as a template. Leonardo Mantilla assisted with invertebrate identifications in Chapter VI. John Feenstra ran the queries to obtain the commercial catch data for Chapter I. I also extend my thanks to Paul Rogers who read and commented on parts of the thesis. Paul Jennings has thought too much about snapper over the past ten years but was a great help in planning and discussing the project and trained me in otolith preparation. Paul Van Ruth, Annelise Wiebkin and Michelle Roberts, my office companions at SARDI, have been a great help in maintaining my sanity since the beginning.

Mum & Dad should be thanked for not asking when it was going to be finished and reading and commenting on the thesis and also, my brother, David, for providing me with plenty of distracting science fiction and British comedy of variable quality.

Kate Hutson assisted in the SAFCOL fridge several times, drew the trawl diagrams (Chapter III) and deserves some considerable praise for putting up with an occasionally cantankerous Richard. She is probably the reason I remained more or less rational in the final stages of the PhD.

Abstract

The population dynamics and fishery productivity of snapper, *Chrysophrys auratus*, in South Australia are strongly driven by inter-annual variation in recruitment. This variable recruitment produces the occasional strong year-class which, over a number of years, results in a cycle of increasing and then decreasing biomass. The aim of this study was to develop an understanding of the recruitment dynamics of snapper through a study of the reproductive biology of adults, as well as the biology and ecology of 0+ recruits. Field sampling was done through 2006 to 2008 in northern Spencer Gulf, the region that generally contributes the majority of South Australia's snapper catch.

The recruitment of 0+ snapper was measured from a study of inter- and intra- annual patterns of distribution and abundance. This was done using two independent trawl sampling regimes, one using a beam trawl and the other an otter trawl, at different times in the settlement season. There was considerable inter-annual variation in abundance of 0+ fish of up to two orders of magnitude and, in some years, almost no recruitment was observed. The spatial pattern of dispersion of recruits was clumped and consistent between years; one area, Western Shoal, always produced the highest catches indicating that it is an important nursery.

The effects of the timing of spawning and water temperature on growth patterns of the 0+ snapper collected in the trawl sampling were studied to determine possible impacts on recruitment processes. Growth was studied from age/length regressions and by measuring the widths of micro-increments in the sagittal otoliths. Sub-surface water temperature was also logged in the region. Growth rate varied inter- and intra-annually but was not limited by temperature in the pre-settlement period. However, post-settlement growth rate was significantly correlated with water temperature and fish exhibited a dramatic slowing of growth as temperature declined in autumn. Later spawned fish were considerably smaller than earlier spawned fish of the same age, which may have implications for post-settlement survival.

The reproductive biology of snapper was studied to determine if annual variation in recruitment was related to egg production. Reproductive samples from northern Spencer Gulf were collected over three seasons (2005/06, 2006/07 and 2007/08) and were analysed macro- and microscopically. Spawning activity was determined by calculating estimates of spawning fraction and batch fecundities. The onset of spawning occurred in November but varied between years and corresponded with times when water temperature was between 18 and 20ºC. The length of the spawning season also differed between years. In each year the peak spawning activity occurred during December when fish spawned almost daily. Spawning frequency and relative batch size did not differ between the first two spawning seasons but, in the third season, batch size was considerably greater and spawning fraction lower. However, recruitment was considerably more variable than the annual differences in spawning output could explain. This indicates that mortality processes during the planktonic or early post-settlement period are important in the recruitment dynamics of snapper.

The impact of water temperature, lunar cycle and tide on the timing and strength of recruitment was investigated. Pre-settlement duration, spawn dates and settlement dates were determined from the

microstructure of the sagittal otoliths of 0+ snapper. The patterns of successful spawning and settlement were determined by back-calculating to the day on which individual recruits were spawned and settled. The frequency distributions of these dates were compared with water temperature, lunar periodicity and the temporal variation in spawning. There was considerable variation within a season in the timing and magnitude of successful recruitment. Strongest recruitment resulted from spawning during December and January on days when water temperatures were between 21 and 23ºC but spawning on days in this range did not necessarily result in recruitment. Pre-settlement duration was unaffected by water temperature. Some evidence of lunar periodicity was detected in both the spawn and settlement date frequencies. Importantly, the spawn date frequency distributions of successful 0+ recruits did not correspond with the measured spawning activity of adults as considerable portions of the spawning season in each year did not produce successful recruits. These results indicated that spawning output and water temperature cannot explain the observed magnitude in recruitment variation.

Food availability for 0+ snapper has been implicated in their patterns of distribution and abundance in New Zealand and Japan. Stomach contents of 0+ snapper were described as an initial step in developing some understanding of the dispersion of 0+ recruits. In spite of their generalist feeding habit, in the area of highest abundance (Western Shoal), snapper took considerably more polychaetes than elsewhere in northern Spencer Gulf. If polychaetes are more abundant at Western Shoal, this could explain the higher density of 0+ snapper there but insufficient information was available on these animals for northern Spencer Gulf to address this hypothesis. Food availability and/or quality may influence the distribution of 0+ recruits.

The multi-species collections from the beam trawls were described to develop an understanding of the spatial dispersion of recruits and their habitat associations. 0+ snapper co-occurred with an assemblage that was characterised by fish and invertebrate species that are associated with mud/soft bottom, but they never occurred with the assemblage of species associated with seagrass, even when recruitment was strongest. This association partly explains the observed distribution pattern, but not all areas of mud/soft bottom had 0+ recruits, even in strong recruitment years. In northern Spencer Gulf, seagrass areas could be excluded from future snapper recruitment surveys.

The recruitment dynamics of snapper in northern Spencer Gulf were characterised by dramatic inter-annual variation but a consistent pattern of dispersion. 0+ snapper were concentrated in a few small areas in northern part of the study region. One of these areas, Western Shoal, appears to be very important as a nursery for snapper. Furthermore, the pattern of 0+ snapper dispersion was independent of recruitment strength. The potential magnitude of 0+ snapper recruitment, set by egg production, was altered by mortality during the early life history. Some of this mortality was related to temperature regimes at the time of spawning but this did not explain all the variation in the magnitude and timing of recruitment. Snapper spawning occurred at times with suitable temperature conditions but recruitment did not always result. This indicates the presence of other factor(s) that have substantial influences on mortality in the early life history.

Chapter I

General Introduction

1.1 Recruitment variation in fishes

Fishery catches and catch rates are not consistent over time but generally demonstrate considerable inter-annual variability (Cushing 1981; Rothschild 1986). Early theories attributed this phenomenon to movement of fish away from fishery areas (Sinclair 1988, 1997). However, in the early 20th Century, the first data on the age structures of fish populations were collected, and indicated that age classes varied in strength and the concept that fluctuation in fish abundance could result from differences in relative year-class strength was conceived (Hjort 1914, 1926; Sinclair 1988, 1997). Many authors have concluded that year-class strength is set very early in the life history (Hjort 1914; Cushing 1975; Houde 1987; Beyer 1989; Bakun 1996), and it is now clear that a major determinant of the dynamics of fish populations, as well as those of many other marine organisms, is variable recruitment of juveniles (Victor 1983; Connell 1985; Doherty and Williams 1988; Roughgarden *et al.* 1988; Sale 1990; Fogarty *et al.* 1991; Doherty and Fowler 1994; Bakun 1996; Levin 1996; Doherty 2002). Thus, factors that cause inter-annual variation in juvenile recruitment will have an effect on year-class strength and ultimately impact on population size and fishery potential.

The commonest form of reproduction in teleost fish is broadcast spawning (Patzner 2008). This reproductive strategy involves the spawning of propagules directly into the water column where fertilisation and egg development take place. Hatching is usually followed by a period of development as a pelagic larva and then, for benthic species, settlement to the bottom (Patzner 2008). Recruitment is usually defined as having occurred at an arbitrary time after settlement (Sale 1990; Fogarty *et al.* 1991). Thus, for this reproductive strategy, inter-annual recruitment variation could result from the interaction of physical and biological processes that influence egg production (Myers and Barrowman 1996), fertilisation rate (Petersen *et al.* 1992) or the mortality of either eggs, larvae (Bailey and Houde 1989) or early post-settlement juveniles (Juanes 2007). Studies of recruitment variation have primarily focused on egg production and egg or larval mortality (Bailey and Houde 1989; Bakun 1996; Cushing 1996),

but the ultimate causes of recruitment variation and the life history stage at which it is determined have been the subjects of debate in both fishery and ecological literature (see Cushing 1988; Sale 1990; Fogarty *et al.* 1991; Bradford 1992; Myers and Cadigan 1993a,b; Marshall *et al.* 1998; Myers 2002).

Does egg production affect recruitment? The most obvious factor that affects egg production is stock size. Intuitively, it seems that a relationship between spawning stock size and recruitment must exist, however, such relationships have been extremely difficult to demonstrate (Rothschild 1986), creating a paradox that has inspired considerable debate (Mertz and Myers 1996; Myers and Barrowman 1996; Myers *et al.* 1997; Gilbert 1997; Rickman *et al.* 2000). The relationship between spawning stock size and the numbers of recruits is often considered to be obscured by pre-recruitment mortality (Cushing 1988), but other factors may affect a stock's egg production (Marshall *et al.* 1998; Witthames and Marshall 2008). The timing and length of spawning seasons, batch fecundities and spawning frequencies vary annually and must influence egg production (Hunter and Macewicz 1985). Thus, fluctuations in such characteristics may cause a population to exhibit radically different patterns of egg production between years, independent of population biomass. This could influence recruitment variation and obscure the relationship between recruitment and stock size (Marshall *et al.* 1998; Witthames and Marshall 2008).

Does egg or larval mortality affect recruitment? The high fecundity of broadcast spawning produces large numbers of potential recruits. Small changes in the rate of mortality in the early life history stages could result in large variations in recruitment (Houde 1987, 1989; Pepin and Myers 1991; Fogarty *et al.* 1991). There are many sources of mortality for these vulnerable life history stages. Starvation and predation are important factors that may determine recruitment and their relative importance has been the subject of some contention (Lasker 1975; Bailey and Houde 1989; Cushing 1990; Gisbert *et al.* 2004). In fact, recruitment variation is the result of the interplay between various life history traits and the environment (Fogarty *et al.* 2001), i.e. the different sources of variation do not operate in isolation. For example, the "stage-duration" hypothesis suggests that fast growing fish benefit over slow growing individuals because they are exposed to high rates of predation for less time (Shepherd and Cushing 1981; Rice *et al.* 1993; Cushing and Horwood 1994). Thus, factors that affect growth rate such as food availability and temperature will interact with predation rates to affect recruitment. Furthermore, the timing of spawning can impact on the temporal match between favourable conditions for growth and survival (Cushing 1990; Mertz and Myers 1994).

The impact of the physical environment on the early life history stages of fish has an impact on recruitment processes (Fogarty *et al.* 1991), which has inspired many investigations into environment-recruitment correlations. In some cases significant relationships were identified, but most have not been validated by subsequent studies (Myers 1998). Although a great deal of effort has been expended looking for environment-recruitment relationships, with the hope of providing a means for predicting future stock size, and thereby better managing a fishery, recruitment predictions are rarely used in managing stocks (Myers 1998). Such predictions probably fail because the factors considered do not operate in isolation. Interactions within and between physical and biological effects confer a great complexity on recruitment processes. Furthermore, with studies that use short time-series of recruitment and enough environmental parameters it is relatively easy to find chance correlations that will not hold when further observations are made (Francis 2006).

The transition phase is a period around the time of settlement when recruitment of pelagic larvae to the benthic habitat occurs (sensu Juanes 2007). For coral reef fishes, this phase has been considered another possible determinant of population regulation (Kaufman *et al.* 1992). Mortality processes during this period may further impact on recruitment dynamics and therefore population structure (Juanes 2007). At this early stage in the life history, distributions are often restricted (Beck *et al.* 2001, 2003). The relative contribution of these areas to the adult population is considered to be the test of their value as nurseries (Beck *et al.* 2001, 2003). However, such a test needs to be done at a time scale that encompasses years of different recruitment strength as the relative contribution of different areas can differ inter-annually (Kraus and Secor 2005). The source of variation in the relative value of nurseries will depend on a variety of interacting biotic and abiotic factors that affect mortality rates (Beck *et al.* 2001). Habitat complexity is considered particularly important for survival when predation is important (Levin 1994; Tupper and Boutilier 1995). However, basic questions such as where do 0+ fish live, in what habitat and on what do they feed are essential questions to address in order to develop an understanding of the impact of these environments on recruitment processes. Furthermore, associations between 0+ fish and different habitats or assemblages determined during periods with variable recruitment can be useful for developing more targeted sampling and to improve precision in estimates of 0+ recruitment strength.

It is now apparent that a complex series of interactions between physical and biological factors during the early life history can result in recruitment variation. Therefore, a detailed knowledge of the early life history and reproductive biology of a species would be required to achieve an understanding of its recruitment dynamics.

Snapper *(Chrysophrys auratus)*

Snapper is a highly significant food fish in Japan, Australia and New Zealand (Foscarini 1988; Kailola *et al.* 1993; Francis 1995). In Japan there is an aquaculture industry as well as a wild fishery (Foscarini 1988; Sudo and Azeta 2001). In New Zealand, snapper is the most significant marine recreational species as well as an important commercial species (Davies and Walsh 1995) and in Australia it is targeted by commercial and recreational fisheries in all mainland states (Kailola *et al.*1993; Fowler *et al.* 2007).

The age structures from commercial catches of snapper in New Zealand (Davies and Walsh 1995) and southern Australia (Coutin 1997; McGlennon 2003) and to a lesser extent along Australia's east coast (Ferrell and Sumpton 1998) have revealed large variations in relative year-class strength. Furthermore, large inter-annual variations of the recruitment of 0+ juveniles are a common feature throughout the range of the species (Japan: Azeta *et al.* 1980a, New Zealand: Francis 1993; Francis *et al.* 1997, Victoria: Hamer and Jenkins 2004, South Australia: Fowler and Jennings 2003). In New Zealand and Japan, snapper are known to be multiple batch spawners with asynchronous oocyte development (Matsuyama *et al.* 1987,1988; Scott and Pankhurst 1992), but no studies have documented this in Australia.

In South Australia, the commercial catch of snapper has shown cyclical variation (Fig. 1.1). Age structures have demonstrated that this is the result of the number and strength of year-classes recruiting to the fished population (Fowler *et al.* 2007). This is thought to relate to the dynamics of recruitment of 0+ fish (Fowler and Jennings 2003; Fowler *et al.* 2007). Historically, the most important region in South Australia for the snapper fishery has been northern Spencer Gulf (Fig. 1.2) (Fowler *et al.* 2007). This region has in most years accounted for >50% and sometimes as much as 75% of the State's catch, in spite of the species' broad distribution throughout the coastal waters of the State (Fig. 1.1). The northern Spencer Gulf is thought to support amongst the highest densities of snapper in Australia (Fowler *et al.* 2007).

Northern Spencer Gulf is known to support both spawning grounds and nursery areas for snapper (Fowler and Jennings 2003; Fowler *et al.* 2005a). Furthermore, a study of the chemistry of snapper otoliths provided evidence that most South Australian snapper, west of the mouth of the River Murray, originate in the northern parts of the two gulfs, particularly Spencer Gulf (Fowler *et al.* 2004; 2005a). For these reasons, this study on recruitment variation, reproductive biology and early life history of snapper was carried out in northern Spencer Gulf.

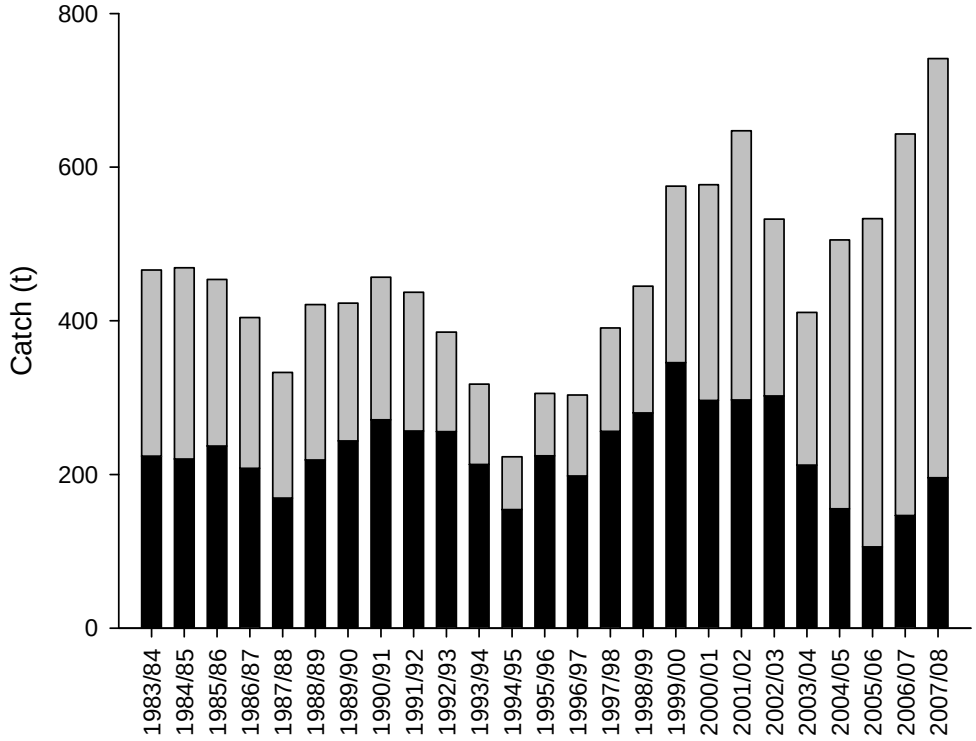


Figure 1.1. Total commercial catch of snapper in South Australia by financial year. Black bars are catch from northern Spencer Gulf and grey bars are catch from the remaining areas of the state.

1.2 Thesis

1.2.1 Aims and objectives

The general aim of this thesis was to develop an understanding of the recruitment dynamics of snapper, *Chrysophrys auratus.* This was achieved through a study of reproductive biology of the population, and the biology and ecology of 0+ recruits in northern Spencer Gulf, South Australia (Fig. 1.2).

The specific objectives were:

i. to describe the patterns of distribution and abundance of 0+ snapper;

ii. to provide information on growth rates of 0+ fish and the relationship between growth and water temperature;

iii. to describe the timing and extent of the spawning season, and how spawning output varies within and between seasons, and to relate patterns of spawning to water temperature;

iv. to determine pre-settlement duration and the effect of temperature on the length of this period;

v. to describe the timing of successful spawning and settlement, based on retrospective analysis of the microstructure of the otoliths, in relation to tide, lunar phase and temperature;

vi. to examine the diet of 0+ snapper, and to determine variation in diet between areas and with fish age;

vii. to describe the dominant features of the species assemblage with which 0+ snapper co-occur.

1.2.2 Thesis Structure

Chapter II provides an introduction to the biology of snapper. It also provides a description of the study region, northern Spencer Gulf and presents some details of the snapper fishery in South Australia.

The intra- and inter-annual patterns of distribution and abundance of 0+ snapper in northern Spencer Gulf based on two independent trawl surveys is described in Chapter III. The results of these surveys were then compared and interpreted in the context of recruitment strength. The fish collected in these surveys were used to assess the effect of water temperature on the early growth by determining the age-length relationships and by analysis of the microstructure of their otoliths. The impact of water temperature on growth was considered in the context of the measured 0+ recruitment.

A detailed study of the reproductive biology of the species in northern Spencer Gulf is presented in Chapter IV. The aims of the study were to measure the spawning activity both within and between seasons and to relate the timing of spawning to water temperature. Key reproductive parameters, such as spawning frequency and batch fecundity, were measured to provide an understanding of the temporal pattern of egg production, both intra- and inter-annually. This provided a context for the analysis of temporal patterns of spawning success measured in Chapter V.

The specific dates on which 0+ snapper recruits captured in the trawl surveys were spawned and subsequently settled to the nursery area form the basis for Chapter V. These data were determined from microstructure of the otoliths of the 0+ fish. The timing of successful spawning and settlement were used to determine the conditions that led to successful

recruitment. The relationships between biological characteristics and environmental conditions were compared between years to account for the inter-annual variation in abundance of 0+ snapper. The spawn dates of successful recruits were compared to the patterns of egg production reported in Chapter IV.

The final two data chapters were studies of the ecology and biology of 0+ recruits. In these chapters, the patterns of distribution and abundance of the 0+ recruits (described in Chapter III) were considered in the context of the assemblages present in northern Spencer Gulf and the prey items taken in different areas. More specifically, in Chapter VI, the diet of 0+ snapper captured in the trawls was assessed to determine whether diet differed among years, spatially or between size classes. The assemblages of teleost fish and macro-invertebrates in northern Spencer Gulf were described in Chapter VII. Those species that most commonly co-occurred or had a discontinuous distribution with 0+ snapper were identified and these data were used to determine surrogate species or assemblages that were indicators of appropriate nursery habitat for 0+ snapper.

The thesis is concluded, in Chapter VIII, with a summary of the key findings, directions for future research and general conclusions.

1.2.3 Notes

Each chapter is written independently, which has involved some repetition between chapters. Water temperature data are repeated in Chapters III, IV and V, but different aspects of these data are emphasised according to the biological processes to which they are being related. There is also repetition of methodologies for otolith preparation between Chapter III and V.

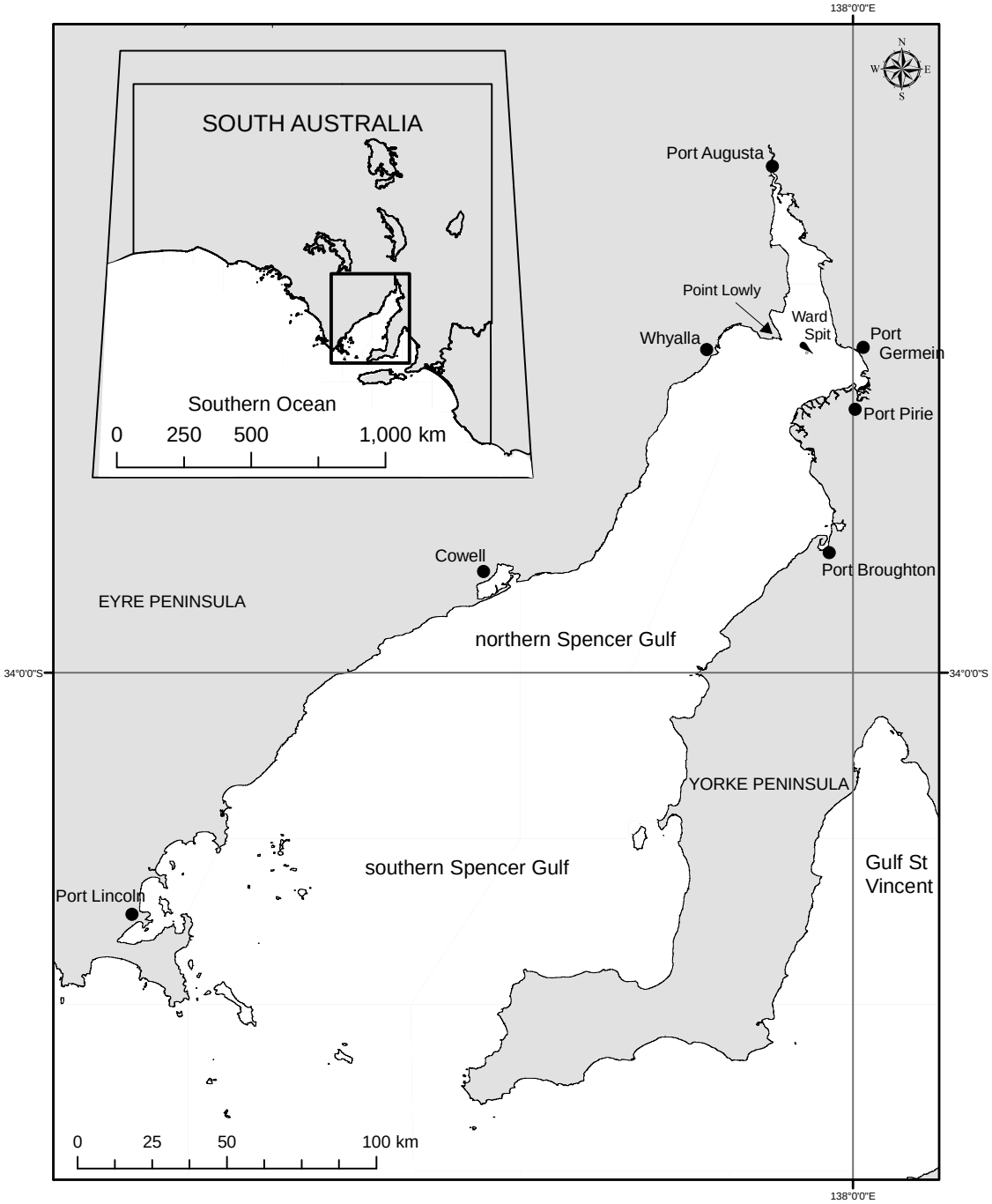


Figure 1.2. Map of Spencer Gulf, inset shows South Australia and region shown in detail is boxed. The study region, northern Spencer Gulf, is the part of the gulf north of the 34ºS line.

Chapter II

Overview of the study species and region

2.1 Snapper (*Chrysophrys auratus* [Forster 1801])

2.1.1 Distribution and Taxonomy

Snapper (*Chrysophrys auratus*) is a member of the family Sparidae (Perciformes: Percoidei). This family includes approximately 115 species that are widely distributed throughout temperate and tropical regions (Nelson 2006; Froese and Pauly 2008), particularly in southern Africa where 44 species occur (Smith and Heemstra 1986; Froese and Pauly 2008). In southern Australia, the Sparidae is represented by only 3 species, the most familiar being snapper (Gomon *et al.* 2008). This species is distributed across the southern half of Australia from Shark Bay in Western Australia to Hervey Bay in Queensland, the North and South Islands of New Zealand, Japan and other parts of south-east Asia, including India (Kailola *et al.* 1993; Gomon *et al.* 2008).

Historically, snapper in Japan and Australasia were considered to represent two separate species. Since the early 1990s, however, many authors have followed Paulin (1990) and used the name *Pagrus auratus*. In contrast, in most Japanese publications the older nomenclature of *P. major* has been retained (Tabata and Taniguchi 2000). Analysis of mtDNA has indicated that the two are very closely related, and are likely to be sub-species (Tabata and Taniguchi 2000). These authors proposed that the Japanese fish be referred to as *P. auratus major* and the Australasian fish as *P. auratus auratus*. They considered the populations to be reproductively isolated, as did Paulin (1990). The genus *Pagrus* has recently been demonstrated to be polyphyletic (Orrell and Carpenter 2004), so Gomon *et al.* (2008) use the generic epithet *Chrysophrys*. For this reason *Chrysophrys auratus* is used here.

2.1.2 General Biology

Snapper are carnivorous and the adults have large crushing jaws with a diverse diet of primarily crustaceans, molluscs and fish (Godfriaux 1974). Size at age varies considerably across the distribution of the species. In South Australia, they grow to a weight of more than 16 kilograms, over 1 metre in length and can attain an age of at least 35 years (Fowler *et al.*

2007). In New Zealand, age estimates of up to 60 years have been reported (Horn 1986; Francis *et al.* 1992).

2.1.3 Early-life History

Snapper spawn pelagic eggs with a diameter of 0.85 to 1.0 mm, have an unsegmented yolk and a narrow perivitelline space (Norris and Jackson 2002). In the laboratory the fertilised eggs hatch after 36 hours at 21ºC. Larvae are approximately 2 mm in length at hatch and do not have functional eyes or mouth (Pankhurst *et al.* 1991). They metabolise their yolk sac for 2 to 3 days prior to first feeding. The larval period lasts from 18 to 32 days and they settle at a length of 8 to 12 mm (Fukuhara 1985; Tanaka 1985; Francis 1994a). Settlement-stage larvae exhibit some selectivity in the timing and location of settlement (Trnski 2002). Viable larvae have been produced by aquaculture processes in water temperatures from 14 to 25.6ºC, with optimal conditions for survival recorded as between 15 and 22ºC (Foscarini 1988).

2.1.4 Population Structure

Snapper are widely distributed throughout the western Pacific with several widely separated populations (Paulin 1990). The Australian distribution of snapper is divided into several stocks. An east coast stock occurs from Wilson's Promontory in Victoria to as far north as Hervey Bay in Queensland (Sanders 1974). There is strong evidence for the presence of further stocks in the southern distribution of snapper. A division exists near the Murray Mouth in South Australia that separates the western South Australian population from the population found in eastern South Australia and western Victoria. This was determined by tagging studies, mitochondrial DNA and analysis of allozymes (McGlennon and Jones 1997). The population structure of snapper in the Great Australian Bight and southern Western Australia is not known.

In Shark Bay, Western Australia, a series of studies has illustrated a complex stock structure of snapper (Johnson *et al.* 1986; Edmonds *et al.* 1989; Bastow *et al.* 2002; Moran *et al.* 2002, 2003). These studies based on tagging, otolith chemistry and genetics show that there is very little exchange between the gulfs of Shark Bay and the adjacent oceanic region, such that they are effectively isolated from each other. This fine-scale stock structure is considered unusual and may be related to the strong salinity gradients that occur in the region (Bastow *et al.* 2002).

2.1.5 South Australian Fishery

Snapper are targeted in the commercial Marine Scale Fishery of South Australia using long-lines and handlines; all net fishing for snapper has been prohibited since 1993. Commercial

catches have been reported in South Australia since 1951-52 (McGlennon and Jones 1997). During the 1980s, commercial catches declined after a series of poor year-classes, with total catch dropping to its lowest level in 30 years in 1994/95. In 1991, extremely strong recruitment of 0+ fish occurred (Fowler *et al.* 2005a), and these recruits entered the fishery during the mid-1990s. The stock was further boosted with another strong recruitment of 0+ fish from 1997. Consequently, the state commercial catch increased to a record level, at the time, of 648 tonnes, that was taken in 2001/02. Since then catches declined briefly before rising again and reaching the current record level in 2007/08 of 741 tonnes which was supported by several age classes.

2.2 Study region: northern Spencer Gulf

South Australia's Gulfs are unique environments. They are large, semi-enclosed inverse estuaries orientated approximately north-south (Fig. 1.2). The larger of these, Spencer Gulf, is approximately 300 km long, extending over ~ 2.5º of latitude, and is 80km wide at the entrance. Northern Spencer Gulf, where this study was done, is the region north of 34ºS (Fig.1.2).

Water temperatures in northern Spencer Gulf range from 11 - 26ºC and salinity can reach levels as high as 45 – 48 ‰ (Shepherd 1983; Nunes and Lennon 1986; Petrusevics 1993). These extremes in temperature and salinity are due to heat exchange over the large intertidal flats that occur throughout the northern gulf, a lack of freshwater inflow and a long flushing time. It also has the greatest daily tidal variation of any part of South Australia, i.e. up to 4.32 m at Port Augusta (Noye 1984). The primary port in the centre of the study region is Whyalla, where daily fluctuations are large by temperate standards, varying by up to 3.1 metres (Flinders Ports 2008).

Northern Spencer Gulf has a central channel north of Point Lowly that is 15 – 20 m deep. In the constriction between Point Lowly and Ward Spit, depth reaches 24 m and a tidal race of around 1.5 knots is charted (Australian Hydrographic Services 2006). To the south the gulf broadens, tidal flats are broad on both eastern and western shores and several large shoals flank the main channel. The main channel south of Point Lowly is marginally closer to the western shore. The channel depth increases gradually to the south reaching a maximum of 30 m in some parts at the southern extreme of the region.

Habitat mapping done in the 1990s indicates that northern Spencer Gulf supported the largest seagrass (mostly *Posidonia* spp.) beds in South Australia (Edyvane and Baker 1996; Edyvane

2000). These seagrass beds were extensive, particularly on the eastern side of the gulf between Port Broughton and Port Pirie. The deeper parts of the gulf (over 15 m) was mostly classified as "bare sand". More recent work did not distinguish between seagrass and unvegetated soft bottom south of Point Lowly but suggested that the deeper areas further north were mostly unvegetated soft bottom (Bryars 2003). There are large areas of mangroves (*Avicennia marina*) at the head of the Gulf; south of Whyalla and near Cowell on the western shore; and at Port Pirie, Port Germein and Port Broughton on the eastern shore. There is very little natural reef in northern Spencer Gulf, although several wrecks provide artificial structure (e.g. "The Leeton" at Whyalla and "The Illusion" off Port Broughton). These are known to support large aggregations of spawning snapper seasonally. There are also numerous smaller artificial reefs including the tyre reefs off Whyalla, Fitzgerald Bay and Port Broughton (Flinders Ports 2008). The only natural reef of any size in northern Spencer Gulf is a small region immediately to the west of Pt Lowly (Hall 2002; Hall *et al.* 2007).

Chapter III

Distribution, abundance and early growth of 0+ snapper, *Chrysophrys auratus*, in northern Spencer Gulf

3.1 Introduction

Variation in relative year-class strength is a common feature of fish populations (Houde 1987). In some extreme cases it results in fish populations that are comprised of only a few strong year-classes (Hjort 1914; Beverton 1962). In a fishery context, this results in catches that vary dramatically depending on the relative strength of the different year-classes that recruit to the population. Thus, to improve fishery management it is useful to measure the relative strength of year-classes before they recruit to the fishery. An early indication of the relative strength of a year-class can be gained by measuring the abundance and distribution of the young-of-the-year recruits (0+ age class) (Houde 1987).

The annual patterns of abundance of juvenile fish can vary at different spatial scales (Huston 1999; Sullivan *et al.* 2000). Thus, to measure year-class strength from abundance patterns requires a robust and extensive sampling regime of the juvenile habitat. Furthermore, different areas can contribute different relative proportions of 0+ fish to an adult population (Gillanders and Kingsford 1996; Gillanders *et al.* 2003) so it is important, particularly for fishery management, to ascertain the relative contribution from different areas (Beck *et al.* 2001). Once the dynamics of the distribution and abundance patterns of 0+ recruits have been determined, more information on recruitment processes can also be obtained by comparing and contrasting inter-annual variation in the early life history traits of the 0+ recruits (Campana 1996).

Variation in recruitment of 0+ fish can result from either inter-annual variation in egg production or environmentally mediated mortality during the early life history. Furthermore, the latter has been hypothesised to be a function of growth rate, with slower growth increasing the potential for mortality (Shepherd and Cushing 1981, Houde 1989). As such, the effects of the physical environment on growth rate may influence the rate of mortality during the early life history and ultimately determine year-class strength (Campana 1996).

Snapper (*Chrysophrys auratus*) is a commercially important species that exhibits variation in year-class strength of more than ten times, and sometimes more, in many parts of its range (Victoria, Coutin 1997; South Australia, McGlennon *et al.* 2000, McGlennon 2003; New Zealand, Davies and Walsh 1995). The catch of snapper in South Australia's Marine Scalefish Fishery depends on the number and strength of year-classes that have recruited to the fishery (Fowler *et al.* 2007). As such, there has been an ongoing research program to study the recruitment dynamics of snapper with one long-term goal of providing an annual recruitment index (Fowler and Jennings 2003). In addition, it is apparent from an otolith chemistry study that most snapper in South Australia originate in the northern parts of South Australia's two gulfs, particularly Spencer Gulf (Fowler *et al.* 2004; 2005b). Furthermore, a broad-scale otter trawl survey has demonstrated inter-annual consistency in the distribution pattern of 0+ fish, but extreme variation in inter-annual estimates of abundance (Fowler and Jennings 2003). The research program has continued since 2003 with the sampling done in the same manner each year, which now provides a 9-year dataset.

Catches of 0+ snapper in these surveys were low for several years (Fowler *et al.* 2005a). There was some concern that the otter trawl may not have been sampling effectively. In order to address this issue a sampling regime utilising a plumb-staff beam trawl, an effective sampler of 0+ snapper in Victoria (Hamer *et al.* 1998; Hamer and Jenkins 2004), was implemented during 2006 and 2007 in conjunction with the otter trawl to expand the sampling effort.

The results of the earlier study also suggested a link between the abundance of 0+ snapper and water temperature (Fowler and Jennings 2003), which supports an earlier finding made in New Zealand (Francis 1993; Francis *et al.* 1997). A mechanism to explain the correlation between water temperature and abundance of juvenile fish is that higher water temperatures result in faster growth rates, reducing their susceptibility to predation and enhancing their ability to feed (Shepherd and Cushing 1981; Chambers and Leggett 1987; Houde 1987). Field evidence for this hypothesis was provided for cod (*Gadus morhua*) where small inter-annual variation in growth rate of young fish, determined from otolith microstructure, explained much of the variation in year-class strength (Campana 1996).

The primary aims of the work presented in this chapter are to describe the intra- and inter-annual patterns of distribution and abundance of 0+ snapper in northern Spencer Gulf; to compare and contrast the estimates of 0+ fish from the two sampling regimes (beam and otter

trawl sampling); to describe the early growth of 0+ snapper and to examine the effect of water temperature on growth.

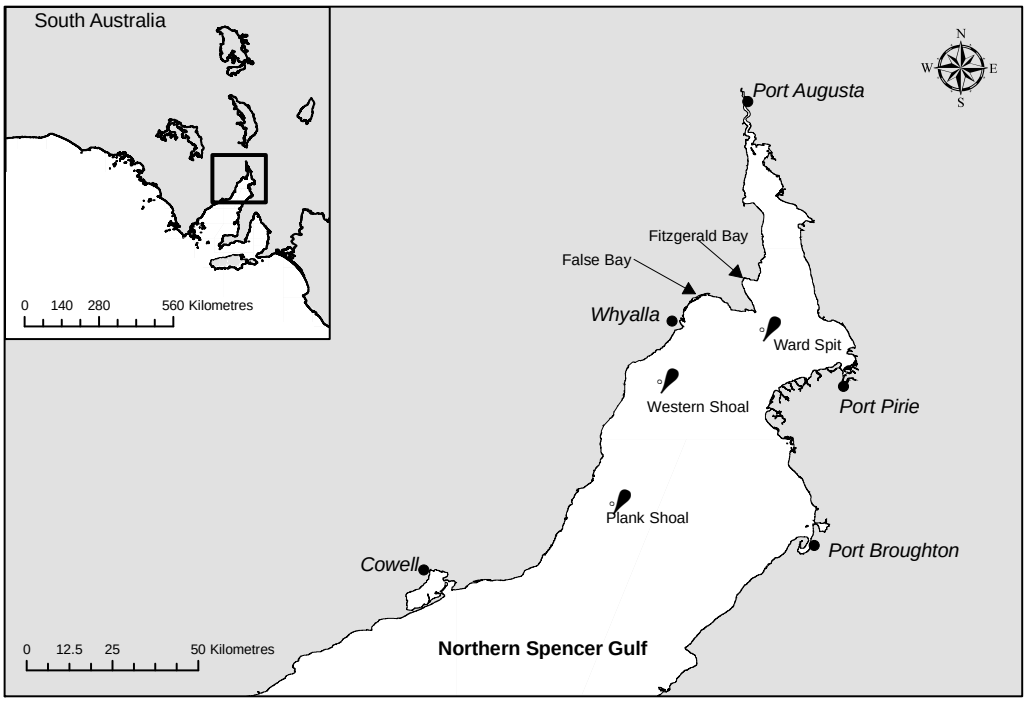


Figure 3.1. Map of the northern Spencer Gulf study region showing the locations of the three temperature data loggers (Ward Spit, Western Shoal and Plank Shoal). The inset shows part of the South Australian coastline with northern Spencer Gulf highlighted.

3.2 Methods

3.2.1 Water Temperature

Water temperatures in northern Spencer Gulf were recorded using temperature data loggers (StowAway TidBit™) at three sites. These were deployed by divers using SCUBA on navigation beacons at Ward Spit and Western Shoal in northern Spencer Gulf on September 20th 2005 and at Plank Shoal on December 9th 2005 (Fig. 3.1). These logged temperature hourly over the study period in depths at high tide of 8 m, 6 m and 5 m respectively. The data were downloaded by divers on November 12th 2006, August 20th 2007 and April 23rd 2008.

3.2.2 Field Sampling Techniques

Sampling for 0+ snapper was done using two independent sampling regimes. One used an otter trawl deployed from a large research vessel (26 m) and the other a plumb-staff beam trawl deployed from a trailer boat (7 m).

Otter Trawl

Sampling was done using a small, purpose built, otter trawl. This net had a headline length of 12.9 m, wing height of 2 m and 12 mm stretched mesh cod end (operating at 70% efficiency, 9 m swept) (Fig. 3.2a). The trawl was deployed from the RV Ngerin and each shot had a fixed duration of 10 minutes from when the net hit the bottom until retrieval. The vessel steamed at 3 to 4 knots and each trawl traversed approximately 1000 m of seabed depending on sea and weather conditions. All sampling was done at night to minimize net avoidance. When the net was retrieved the contents were sorted and any 0+ snapper were collected. These were frozen on board at -30ºC soon after capture.

The otter trawl sampling was done in early April in every year from 2000 to 2008. The trawl shots were divided into four areas: Western Shoal, False Bay, Fitzgerald Bay and Southern (Fig. 3.3). The number and position of shots in each area varied slightly between years (see Results section for detail). A major change in the sampling regime was implemented for the last 3 years, when all shots south of 33.5ºS were excluded from the sampling as no 0+ snapper had been captured in any of those shots during the first six years. This halved the sampling effort in the Southern Area.

NOTE:
These figures are included on page 16 of the print copy of the thesis held in the University of Adelaide Library.

Figure 3.2. (a.) Otter trawl used to sample 0+ snapper in northern Spencer Gulf; dimensions in the text. Adapted from Carrick (2003). (b.) Beam trawl used to sample 0+ snapper in northern Spencer Gulf; dimensions in the text. Adapted from Hamer and Jenkins (2004).

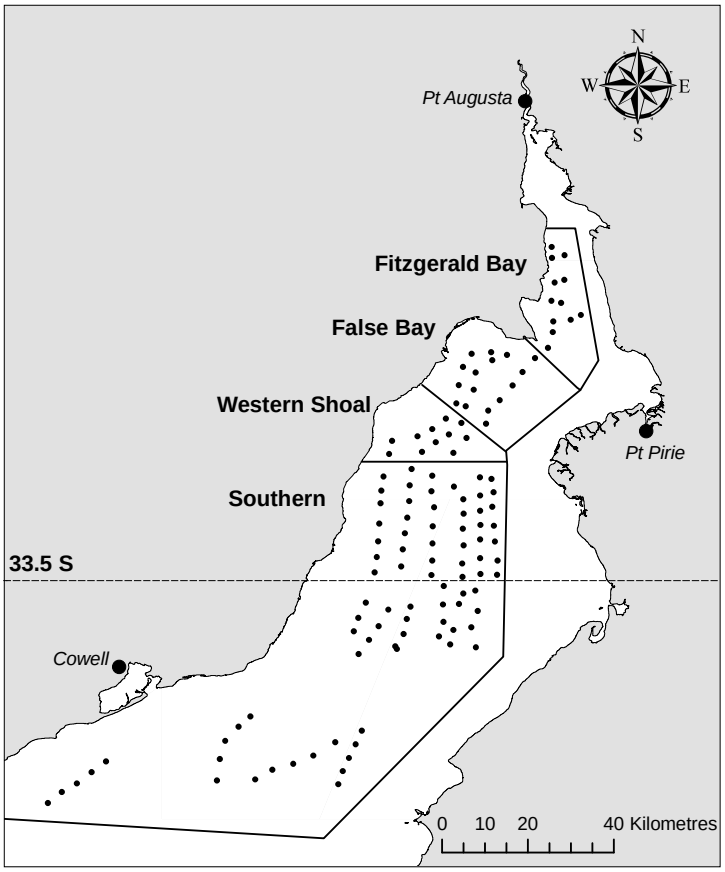


Figure 3.3. Map of northern Spencer Gulf showing the position of the stations sampled during the otter trawl sampling and the areas used to describe distribution and abundance patterns.

Beam Trawl

A plumb-staff beam trawl with a 3 m beam, 4 mm^2 knotless mesh in the body and 3 mm^2 in the cod end was used in this study (Fig. 3.2b). The net was based on the design used to sample juvenile snapper in Port Phillip Bay (Hamer *et al.* 1998; Hamer and Jenkins 2004), with some modifications: a rubber mat was attached to the underside of the cod end to protect the mesh from contact with the bottom; a stainless steel cable was used on the lower bridles; a central rope was used to support the beam; and no emergency retrieval line was attached in order to simplify deployment.

The net was deployed from the RV Odyssey, a 7 m shark-cat, and towed at a speed of 1.5 to 2 knots. Each trawl had a fixed duration of 5 minutes from when the net made contact with the bottom until retrieval was initiated, and traversed approximately 300 metres of seabed depending on sea and weather conditions. To ensure the net was on the bottom for the five minute duration of the trawl, a time-depth logger was attached to the net in 2007. This confirmed that the net was making contact with the bottom for the duration of the trawls. All sampling was done at night to minimise net avoidance. The catches were processed

immediately after retrieval and the 0+ snapper were stored on ice on the vessel. They were frozen on return to shore each morning.

At the beginning of the study, sampling was planned for 4 locations with 9 replicate trawls at each location at each of two times (early and late in the settlement season - Table 3.1 for dates). The study locations were False Bay, Fitzgerald Bay, Ward Spit and Western Shoal (Fig. 3.1). Ward Spit was selected on the basis of anecdotal evidence that high abundances of 0+ snapper had occasionally been found there and the remaining locations were selected on the basis of distribution patterns observed from the otter trawl sampling (Fowler and Jennings 2003). During the early sampling, only 7 shots were successfully completed in False Bay due to gear difficulties, but 9 shots were completed at each other location. In the second survey, 9 shots were achieved for each location (Table 3.1). Furthermore, during 2006, Western Shoal was sampled but it became clear from the otter trawl results that the beam trawl shots had been undertaken in an area that was too far north. Consequently, a final survey was undertaken in May that only sampled at Western Shoal, to ensure that the net was fishing effectively and to identify suitable locations for the following year.

In 2007, the intended sampling regime was not tractable, due in part, to steaming time between trawl stations, the rough nature of the bottom in False Bay and the predominance of south-easterly winds during February. In this year, False Bay was not sampled on either occasion and three extra trawl shots were assigned to each of the other locations (Table 3.1). The placement of individual shots is indicated in the Results section.

Table 3.1. Details of surveys from R.V. Odyssey using the plumb-staff beam trawl for 2006 and 2007. For locations of individual trawls see distribution maps in Fig. 3.6.

Year	Survey	Location	Number of trawls
2006	Survey 1 (27th February to 3rd March)	False Bay	7
		Fitzgerald Bay	9
		Ward Spit	9
		Western Shoal	9
	Survey 2 (4th - 6th April and 9th - 10th April)	False Bay	9
		Fitzgerald Bay	9
		Ward Spit	9
		Western Shoal	9
	Survey 3 (10th - 11th May)	Western Shoal	6
2007	Survey 1 (20th - 23rd February)	Fitzgerald Bay	12
		Ward Spit	12
		Western Shoal	12
	Survey 2 (19th - 22nd March)	Fitzgerald Bay	12
		Ward Spit	12
		Western Shoal	12

3.2.3 Laboratory processing techniques

Between 2006 and 2008, all 0+ snapper captured by either method were measured for caudal fork length (CFL) from the tip of the snout to the posterior end of the middle caudal rays, to the nearest mm. They were weighed to the nearest 0.01 g. The sagittal otoliths were removed, cleaned of extraneous tissue and dried by rubbing on silk cloth. The otoliths were then used to determine the age of each fish.

Otolith preparation

Transverse sections of the sagittae are the best preparation to expose the microstructure of the otoliths and age juvenile snapper (Fowler and Jennings 2003). As such, this ageing technique was used in this study. The transverse sections were prepared by grinding and polishing to expose the internal microstructure. One sagitta from a fish was mounted on a microscope slide using CrystalBond™. It was then ground from the anterior end towards the core using a Gemmasta grinding wheel with a 45 μm diamond sanding disc and then polished on 9 and 6 μm imperial lapping film. The polished surface was then mounted at the centre of a microscope slide after which the grinding and polishing was done from the posterior end to produce a section of ~50 μm thickness. In some cases, a final polish was done using 0.05 μm alumina powder on suede cloth.

Otolith Analysis

A transverse section for one sagitta from all fish was prepared. These were examined using an Olympus compound microscope at magnifications of 400x to 1000x, with the image displayed on a computer screen via a video camera and Optimas image analysis software. Immersion oil was used to enhance the image by clearing the surface scratches. A count of the post-settlement increments was made from the settlement mark to the proximal surface between the sulcus and the ventral apex along the dark band identified as the sagittal-subcupular meshwork fibre zone (SMF; Francis 1994b) (Appendix 1), which was the axis that provided the clearest sequence of micro-increments at 400x. The pre-settlement increments were counted from the primordium in the opposite direction to the SMF line to the settlement mark at 1000x (Fowler and Jennings 2003; Appendix 1).

Increments were counted blind, with respect to fish length, and each otolith was examined on three separate occasions. If the counts differed by more than 5% the otolith was rejected, otherwise the mean was accepted as the best estimate of the count, retaining the separate counts of pre- and post-settlement increments. The age of the fish was calculated by summing the pre- and post-settlement increments, but with the addition of four days to

accommodate for two days of egg development and that no increments form for two days after hatch (Pankhurst *et al.* 1991).

3.2.4 Statistical analyses

The catches of 0+ snapper from the beam trawl sampling were compared among years, locations and surveys using analysis of variance (ANOVA). Factors were fixed and the design orthogonal. False Bay was excluded from the analysis because it was not sampled in 2007. Survey 3 (May 2006) was also excluded because it was done only in one year. Thus, a three factor ANOVA comparing Years (2) Locations (3) and Surveys (2) was done. The raw data were not normally distributed (Kolmogorov-Smirnov test $P<0.01$) and variance was heterogeneous (Levene's test $P<0.01$). As such, the data were transformed by ln (x+1) but the assumptions were still violated, although the heterogeneity of the variance was considerably reduced. Since ANOVA is robust to violations of these assumptions when sample sizes are large, the analyses on the transformed data were still considered (Underwood 1997). The design was, however, unbalanced and to maintain a conservative approach, p-values were set at 0.01.

The variation in CFL and age of 0+ snapper captured in the otter trawl were compared between 2006 and 2007 by ANOVA. As only three 0+ snapper were collected from the otter trawl in 2008 it was excluded from the analysis. The variation in the distributions of CFL and age of 0+ snapper captured in each beam trawl survey were also analysed by ANOVA. Distributions were normal (Kolmogorov-Smirnov test $P<0.01$) for all surveys, but variances were heterogeneous (Levene's test $P<0.01$). As sample sizes were large and ANOVA is robust, the analyses were done on the untransformed data and p-values were set at 0.01. When significant differences were found, post-hoc Tukey's tests were used to determine which means differed.

Growth was described by the relationship between fish size and age. Regression analysis of age and growth was also done for the fish from the beam trawl surveys and the otter trawl surveys for 2006 and 2007. This procedure describes the average daily growth rate for the size range of fish captured, regardless of when they were spawned throughout the season. Intra-annual variation in these relationships was examined by analysis of covariance, comparing the regressions between surveys each season. The inter-annual variation in these relationships was considered by analysis of covariance, comparing the regressions of the otter trawl surveys for 2006 and 2007.

A more refined examination of growth rate was done using back calculation (Campana and Jones 1992) and the results used to consider the relationship between daily growth and temperature. The suitability of back calculation was tested by investigating the relationship between fish size and otolith size for a random sample of 71 fish from across all surveys. Otolith size (O_f) was the sum of the increment widths (I_w) measured from the primordium to the outer edge of the otolith along the curved axis of maximum growth (Fowler and Jennings 2003), as measured on a third examination of the transverse section of the sagitta. The increment widths were used to estimate increments of daily somatic growth throughout the lives of the fish using the following equation: Daily somatic growth = $(I_w/O_f)*(L_f-L_h)$, where O_f is otolith size, L_f is caudal fork length and L_h is length at first increment formation, i.e. 2.6 mm (Fowler and Jennings 2003). These data were used to test the effect of the time of spawning on daily somatic growth rate (DSG). This was done by selecting 5 fish from each of 3 different periods, i.e. early, middle and late, from the spawning seasons of 2005/06 and 2006/07 (Table 3.2). The fish for each of these groups were chosen as having the least spread of spawn dates possible (Table 3.2). DSG was averaged for each day across the five fish in each group.

Table 3.2. Attributes of samples of 0+ snapper used in the determination of somatic growth increments through back calculation.

Season	Timing of origin	Sample size	Mean (±s.e.) age (days)	Mean (±s.e.) size (mm)	Timing of spawning
2005/06	Early	5	110 ± 0	66.6 ± 0.51	15th Dec 2005
	Middle	5	107.8 ± 8.25	56.2 ± 3.14	1st Jan 2006
	Late	5	93.2 ± 8.29	47.0 ± 4.39	15th - 17th Jan 2006
2006/07	Early	5	121.4 ± 4.39	83.2 ± 3.38	8th - 10th Dec 2006
	Middle	5	100.6 ± 9.70	63 ± 7.04	21 - 27th Dec 2006
	Late	5	76.8 ± 4.60	42.8 ± 2.31	7th - 9th Jan 2007

To determine if there was a relationship between DSG and temperature the daily time series of somatic growth and average daily water temperature were subject to cross-correlation analyses (Chatfield 1996), at lag 0 for each group (early, middle and late season). Then, the relationship between DSG and water temperature was described for both pre- and post-settlement periods using regression analyses. The relationship was best described using the natural log of DSG. This was done for the data pooled across each group. The division into pre- and post-settlement periods was made on the basis that all of the fish used in these analyses had settled by age 25 days.

3.3 Results

3.3.1 Water temperature

Data were recorded continuously from Plank Shoal from the 9th December 2005 and from Ward Spit and Western Shoal from the 20th September 2005. The data were retrieved twice each year until a final download on the 17th April 2008. Water temperature varied between sites, with the highest and lowest temperatures recorded at the northernmost site, Ward Spit (Fig. 3.4a). The highest temperatures in each year were recorded in late January and early February at which time the average difference between the northern and southern sites was 1.48ºC. The largest difference between sites was recorded on 23rd January 2006, which was also the date of highest recorded water temperature during the study of 26.86 ºC at Ward Spit (Fig. 3.4a). The temperature data presented in the following sections are those logged at Western Shoal (Fig. 3.4b) because it was closest to where most 0+ snapper were collected.

3.3.2 Otter Trawls

Distribution and abundance

The catches of 0+ snapper varied dramatically among years (Fig. 3.5). In the first three years the lowest catch of a total of 8 fish was recorded in 2002 and the highest catch was 164 fish in 2000 (Fowler and Jennings 2003). Since then, even greater variation in abundance has been observed. The highest catch of 253 fish was taken in 2006 and only a single individual was captured in 2005 (Fig. 3.5).

Three main areas have regularly contributed to the catch of 0+ snapper in the otter trawl sampling, i.e. Western Shoal, False Bay and Fitzgerald Bay (Fig. 3.6). No 0+ snapper were captured south of 33.5ºS between 2000 and 2005. As such, these trawl shots were dropped from the sampling regime from 2006 to 2008. The area immediately south of Western Shoal (Fig. 3.6) has consistently returned the highest catches, with the exception of 2008. Even in 2005 the solitary 0+ snapper was captured in this area. Furthermore, regular captures have been made in False Bay and Fitzgerald Bay (Fig. 3.6).

These areas, depicted in Figure 3.3, represent a natural division to consider the spatial consistency of the inter-annual abundance patterns. All these areas returned zero catch in some years (Fig. 3.6 and 3.7). The highest average contribution was from Western Shoal (66% of all fish). False Bay and Fitzgerald Bay both contributed significantly in some years but False Bay usually contributed more (Fig. 3.7). The Southern Area contributed least to the catch.

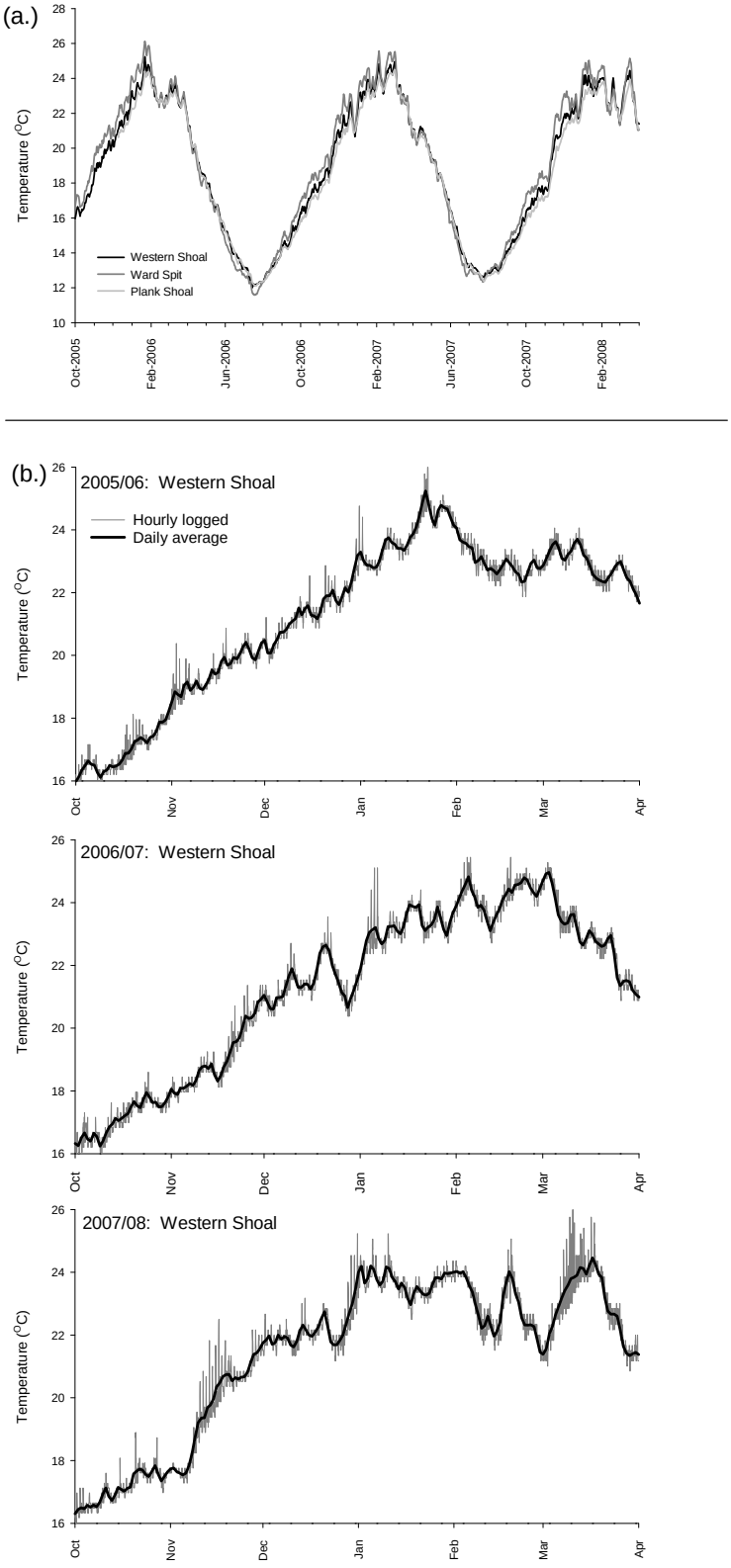


Figure 3.4. Water temperature data from northern Spencer Gulf (a.) Daily average water temperature from three locations in northern Spencer Gulf between late 2005 and April 2008. (b.) Daily average and hourly recorded data for Western Shoal for October to April for 2005/06, 2006/07 and 2007/08.

The inter-annual pattern of abundance was generally consistent between areas, with one notable exception. The extremely high abundances recorded at Western Shoal in 2006 were not reflected in the other areas (Fig. 3.7). Total catches from False Bay in 2006 (14 snapper) were considerably lower than for 2000 (21 snapper) and 2001 (46 snapper) and in 2008 no fish were captured at Western Shoal.

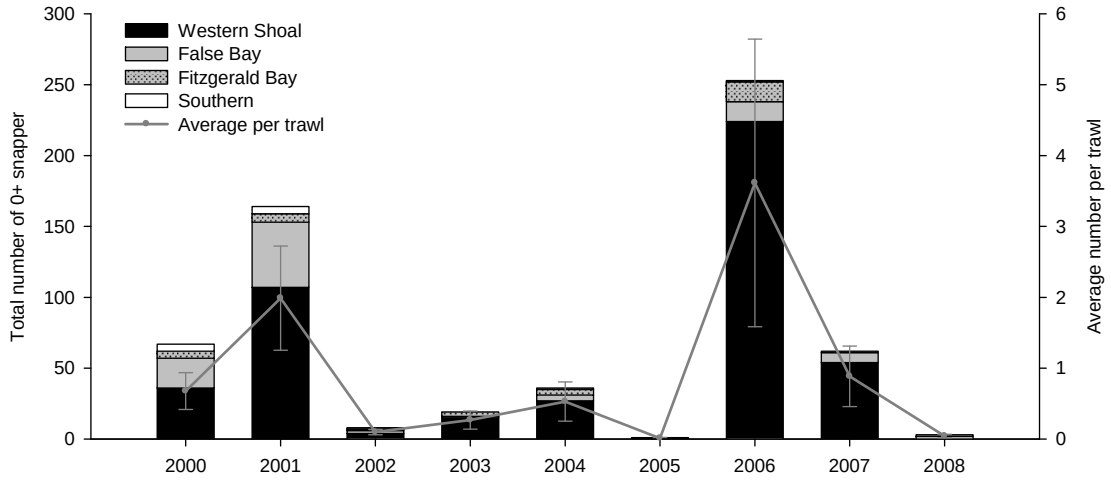


Figure 3.5. The total number of 0+ snapper captured in each location by year and the average number of snapper caught in trawls north of 33.5ºS

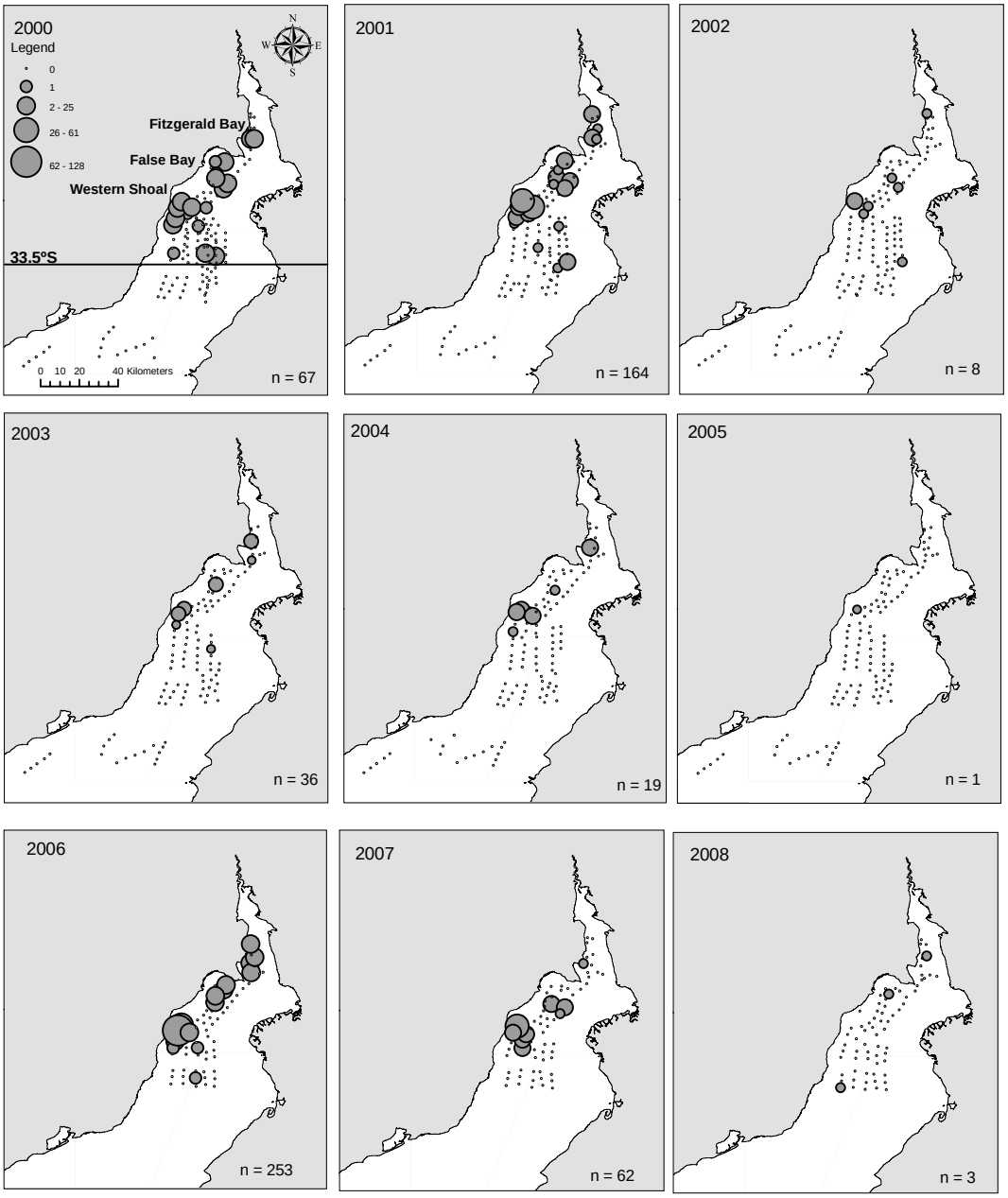


Figure 3.6. The results from sampling of 0+ snapper using the otter trawl in April of each year from 2000 to 2008 showing the location and numbers of fish per trawl. Note that the 2000 to 2002 results are repeated from Fowler and Jennings (2003).

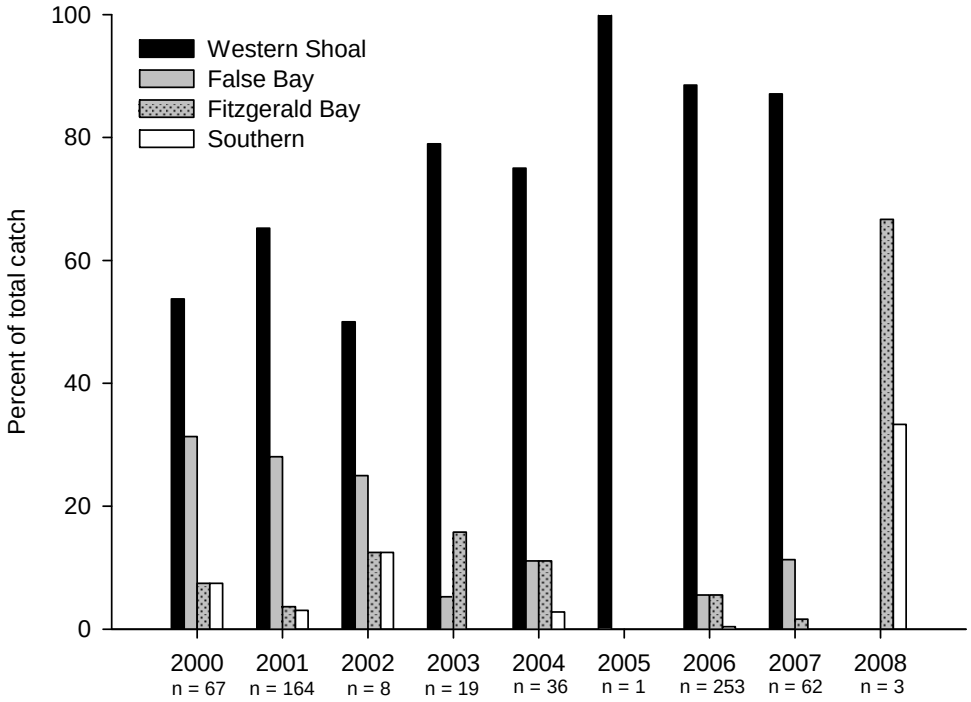


Figure 3.7. The relative contribution of each area to the total catch of 0+ snapper in the otter trawl surveys each year. Areas are illustrated in Figure 3.3.

Length and age frequency

In 2006, a relatively large number of fish were collected (n=253), which had a size distribution with 2 distinct peaks at 53 and 63 mm CFL, and a smaller one at 82 mm CFL (Fig. 3.8a). The mean (± s.e.) fish length was 54.71 ± 0.86 mm CFL (Table 3.3). The age distribution also had 2 peaks at 89 and 105 days and a third of lower magnitude at 118 days (Fig. 3.8b). In 2007, the 59 fish collected ranged from 38 to 101 mm CFL (Fig. 3.8). The latter was the largest 0+ snapper caught in the sampling. The mean size (± s.e.) was 75.03 ± 2.12 mm CFL (Table 3.3). The ages ranged from 79 to 130 days but most were from 105 to 125 days. In 2008, only three 0+ snapper were captured. Their lengths were 29, 42 and 49 mm CFL with ages of 60, 78 and 87 days, respectively (Fig. 3.8). The fish captured in the otter trawl in 2006 were significantly younger and smaller than those caught in 2007 (Age, $F_{1,297} = 91.943$ $P<0.001$; CFL, $F_{1,312}=102.371$ $P<0.001$) (Table 3.3). The shapes of the age and size frequency distributions mirror each other indicating that size and age were closely related.

Table 3.3. Means and ranges of caudal fork lengths and ages for 0+ snapper captured in each survey.

Net	Year	Survey	Mean CFL (mm) ± s.e.	Range CFL (mm)	Mean age (days) ± s.e.	Range ages (days)
Beam trawl	2006	1	44.90 ± 6.69	28-63	74.00 ± 4.69	53-93
		2	45.56 ± 3.67	18-77	80.67 ± 3.90	46-111
		3	60.32 ± 2.11	46-85	125.82 ± 2.17	111-153
	2007	1	41.60 ± 1.55	36-50	65.00 ± 2.27	58-77
		2	50.05 ± 2.78	29-72	80.20 ± 2.42	65-101
Otter trawl	2006	-	54.71 ± 0.86	23-92	93.96 ± 0.89	53-121
	2007	-	75.03 ± 2.12	38-101	118.57 ± 5.52	79-130
	2008	-	40.00 ± 5.86	29-49	75.00 ± 7.94	66-87

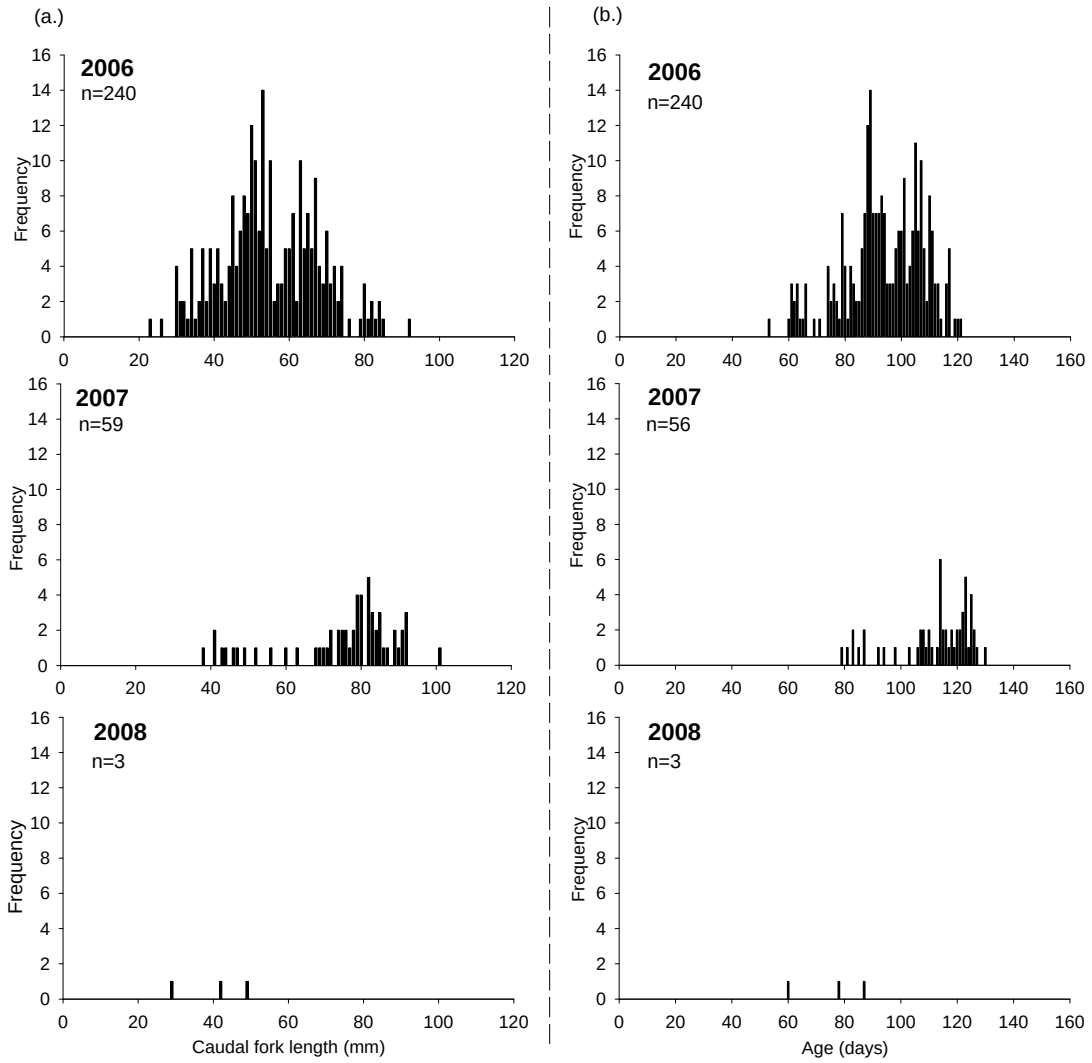


Figure 3.8. (a.) Size-frequency distributions for the 0+ snapper captured in each of 2006, 2007 and 2008, with sample sizes shown. (b.) Age-frequency distributions for the 0+ snapper captured in the otter trawl surveys in 2006, 2007 and 2008, with sample sizes shown.

3.3.3 Beam Trawls

Distribution and abundance

The total catch of 0+ snapper per survey ranged from 8 to 23 fish. The highest densities of 0+ snapper occurred in 2006 at Western Shoal during survey 3 and at Ward Spit in survey 2, when maximum catches per shot were 8 and 6, respectively (Fig. 3.9). At all sampling times and locations, with the exception of May 2006, numerous shots caught no 0+ snapper, whilst successful shots were usually adjacent to each other, within a location (Fig. 3.9).

The annual abundance of snapper was not consistent between locations (year*location interaction; $F_{2,114} = 6.788$ $p<0.01$). Abundances were lower at Ward Spit and Fitzgerald Bay in 2007 but did not change at Western Shoal. This is because sampling done at Western Shoal in 2006 was further north and on different habitat than in 2007. The change in the position of the shots was made because the results of the otter trawl survey for 2006 indicated that the area used by 0+ snapper was further south than had been sampled. Thus, the interaction may be an artefact of the alteration in the sampling design between 2006 and 2007 at Western Shoal. There was a significant intra-annual temporal effect on abundance (Survey; $F_{1,114} = 7.032$ $p<0.01$). This effect is clear from Figures 3.9 and 3.10 in that more snapper were caught in survey 2 than survey 1 in each year.

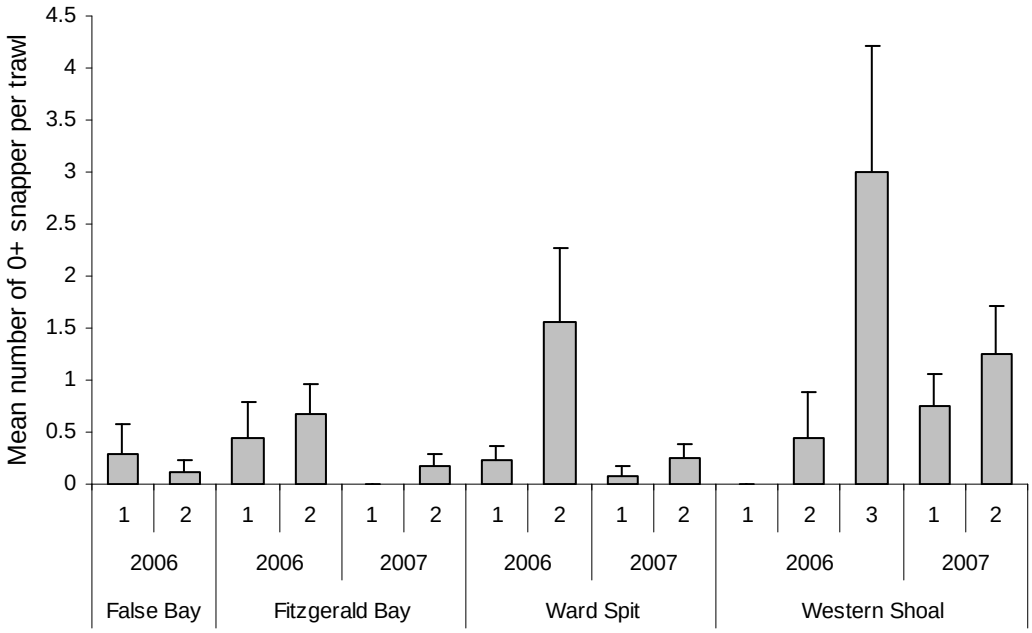


Figure 3.9. The mean number of 0+ snapper caught for each survey in each year for all locations, error bars are standard errors. Note that trawls traversed ~900m^2 of seabed.

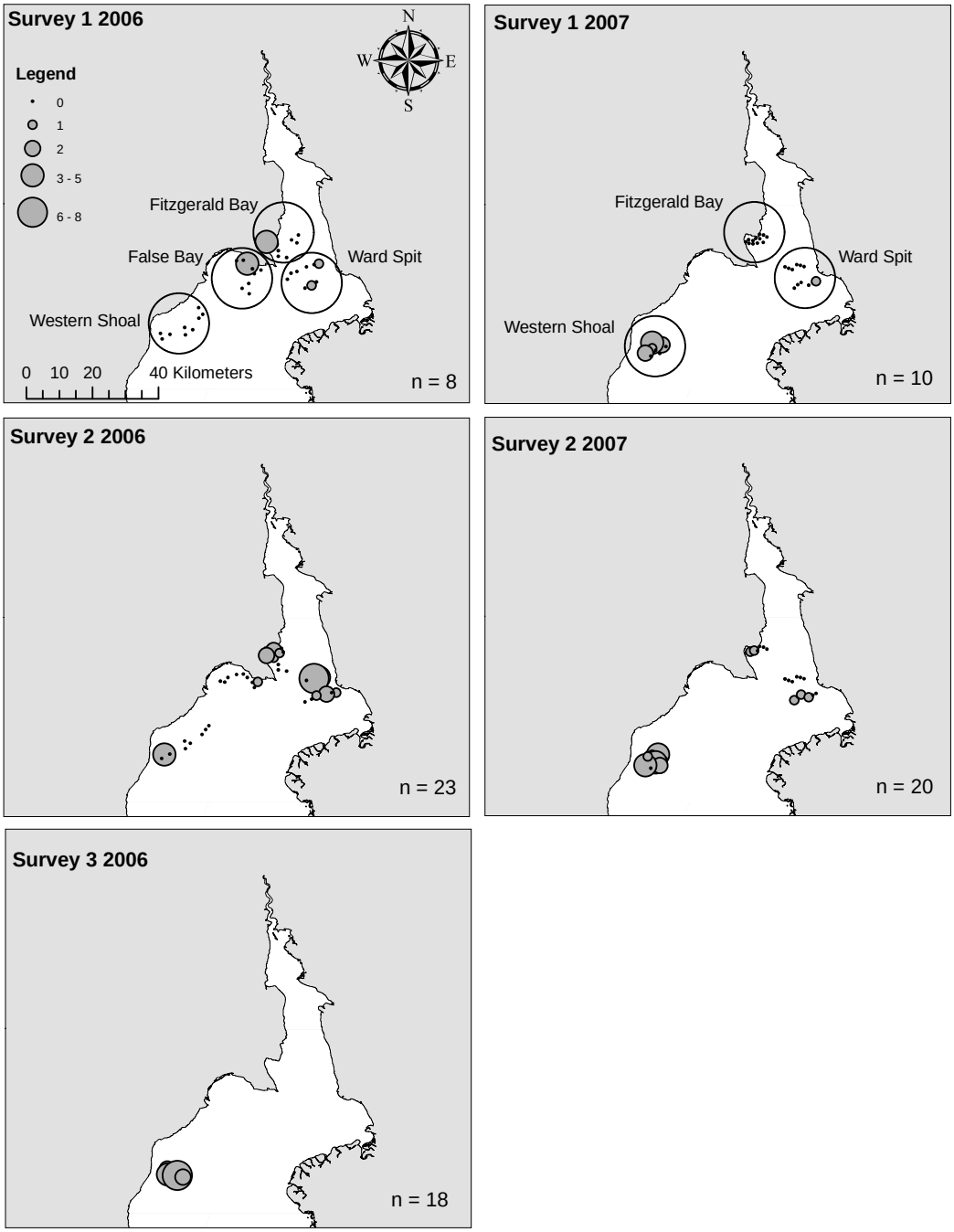


Figure 3.10. Results from sampling 0+ snapper in each beam trawl survey showing the location and numbers of fish per trawl. The groups of trawl shots are circled in the first map for each year.

Length and age frequency

The size and age distributions differed between surveys (Figs. 3.11 and 3.12). The smallest fish captured was 18 mm CFL and was also the youngest at 46 days (Table 3.3). The largest and oldest fish captured in the beam trawl were caught in survey 3 of 2006 with a mean CFL of 60.32 mm and mean age of 126 days (Table 3.3). The fish were generally smaller and younger in the first beam trawl survey each year than the second (Table 3.3). However, the range of ages was also broader in the second survey each year as it also included some small, young fish (Figs. 3.11 and 3.12; Table 3.3).

Fish size (CFL) differed between the surveys ($F_{4,80}$=5.194, p=0.001), as did age ($F_{4,79}$=55.225, p<0.001). Post-hoc Tukey's tests identified several differences (Fig. 3.13). Only two comparisons of mean length were significantly different. The third survey in 2006 differed from both the second survey in 2006 and the first in 2007. Significantly, the mean size of fish collected in the first and second beam trawl surveys did not differ in either year, however, they did differ in age in 2007. Furthermore, the fish captured in the beam trawl sampling in May 2006 were significantly older than fish captured in any other Survey.

3.3.4 Growth analysis

Age-Length Regressions

In 2006 and 2007, the relationships between age and length were linear for all surveys (Fig. 3.14). In 2006, the slopes of the regressions were not significantly different between these surveys, however, a significant difference in intercepts was detected (Table 3.4a). The intercept for survey 3 was much lower than for the other surveys (Fig. 3.14). There was also a trend for the intercept of the regression to decrease the later in the year that the sampling was conducted. In 2007, no difference in slope was detected, but the intercept differed significantly between surveys (Table 3.4a). The first survey intercept was much higher and the slope lower, suggesting a slower growth rate, although sample size was low (n=10; beam trawl survey 1). There was a trend for the intercept of the regression to be lower the later in the year the survey was done, as in 2006. Not enough fish were captured in 2008 for meaningful regression analyses, however, CFL increased with age.

To compare inter-annual growth patterns the age-length regressions developed from fish sampled using the otter trawls in 2006 and 2007 were subject to ANCOVA. The slope, i.e. instantaneous growth, was 0.87 mm.d-1 in 2006, significantly lower than the estimate of 0.99 mm.d-1 in 2007 (Table 3.4b.). This is evident when the average size of a 120-day old fish was calculated from each equation. In 2006, such a fish was 77.5 mm CFL, smaller than an equivalent fish from 2007, at 81.1 mm.

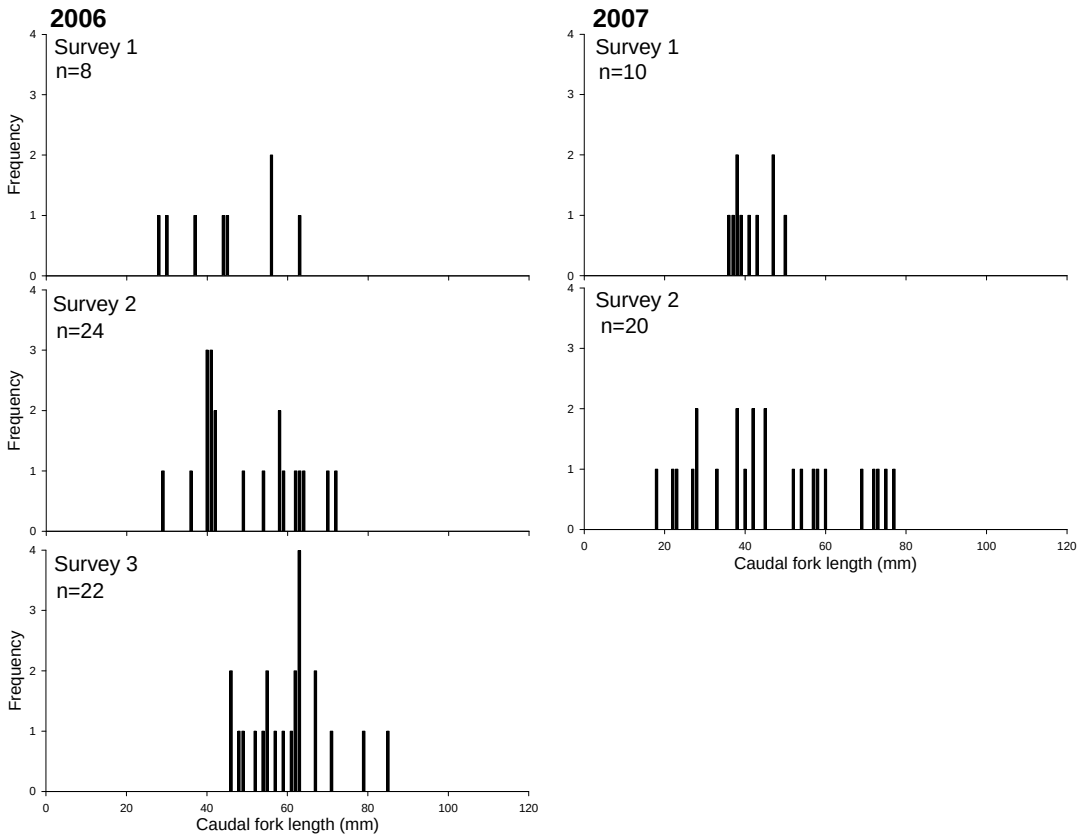


Figure 3.11. Size frequency distributions of 0+ snapper captured in each trawl survey with the sample sizes shown.

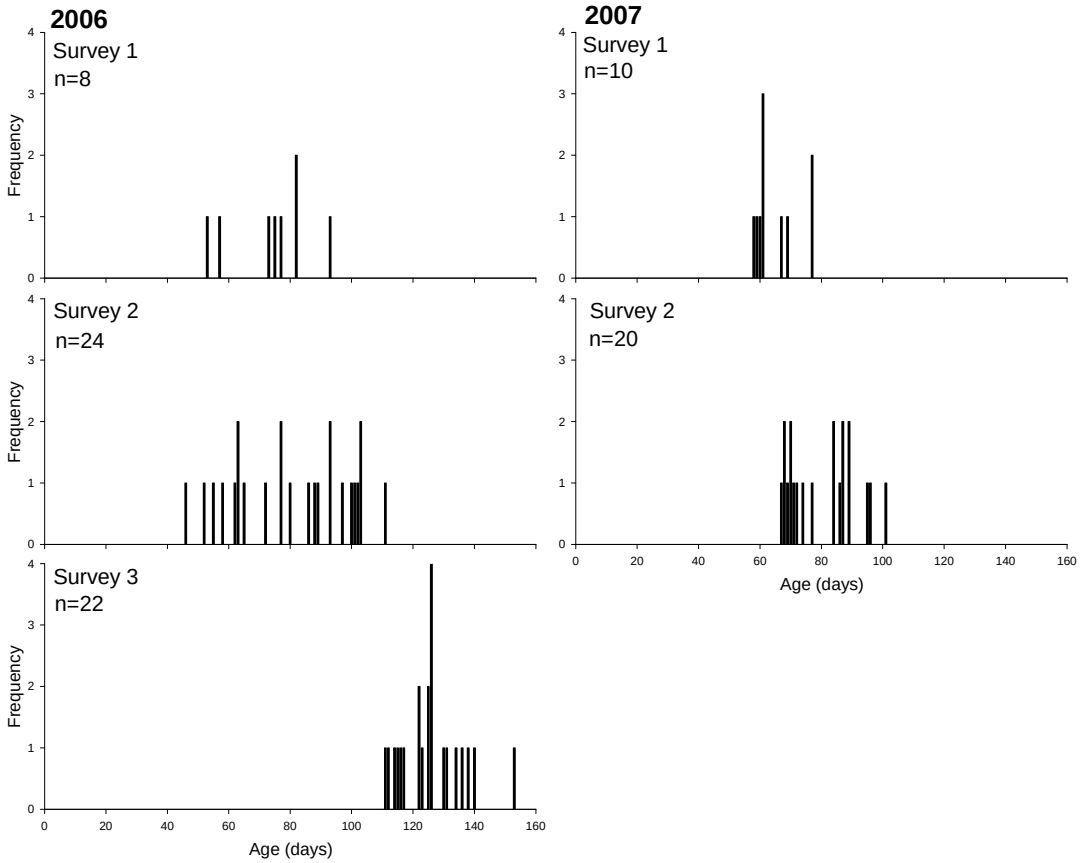


Figure 3.12. Age frequency distributions for 0+ snapper captured in the beam trawl surveys in 2006 and 2007, with sample sizes shown.

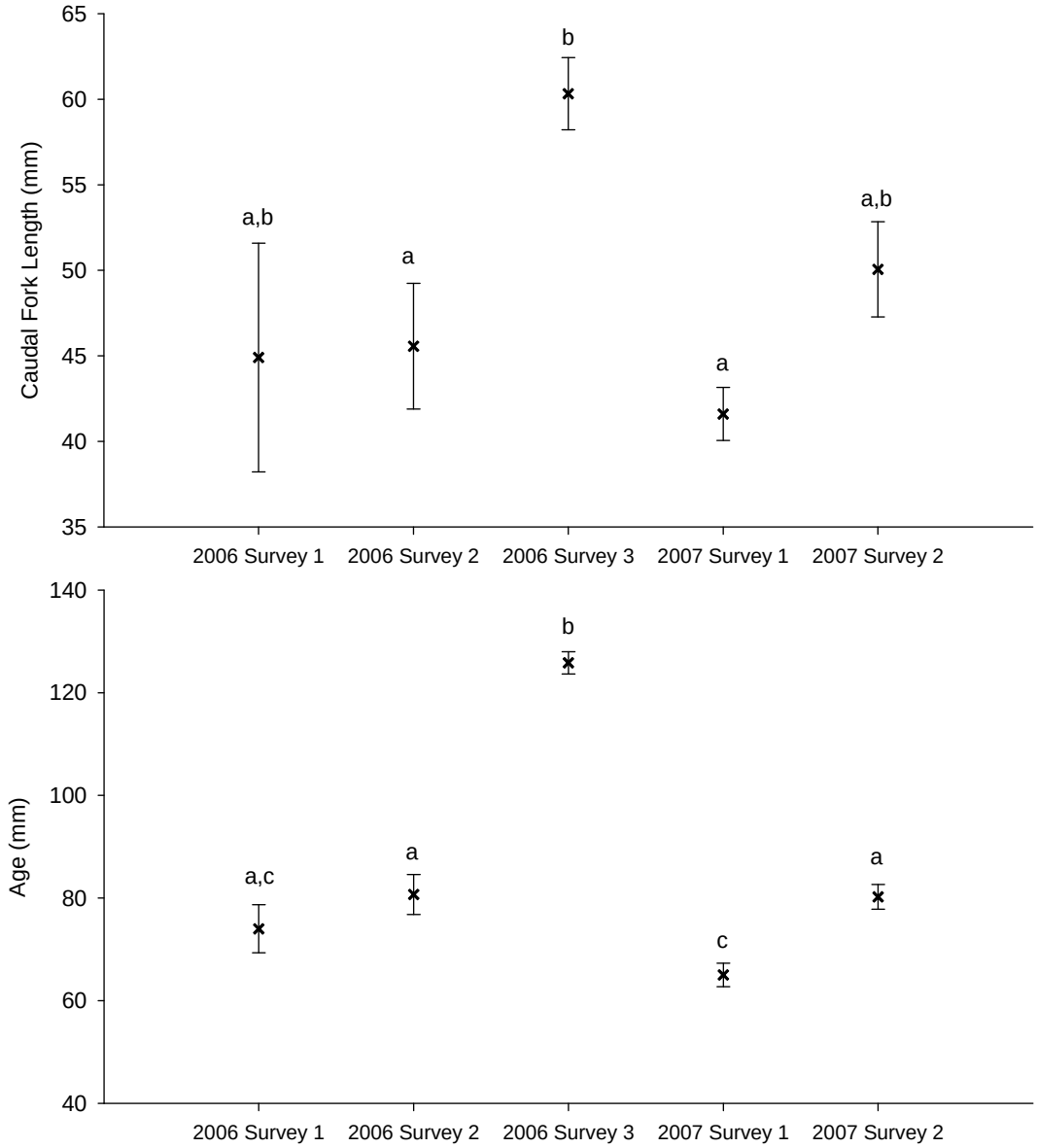


Figure 3.13. Mean and standard error of caudal fork length and age of fish captured in the beam trawl surveys. Letters indicate those means not-significantly different from each other, as determined by post-hoc tests. (i.e. those that share the same letter were not significantly different.)

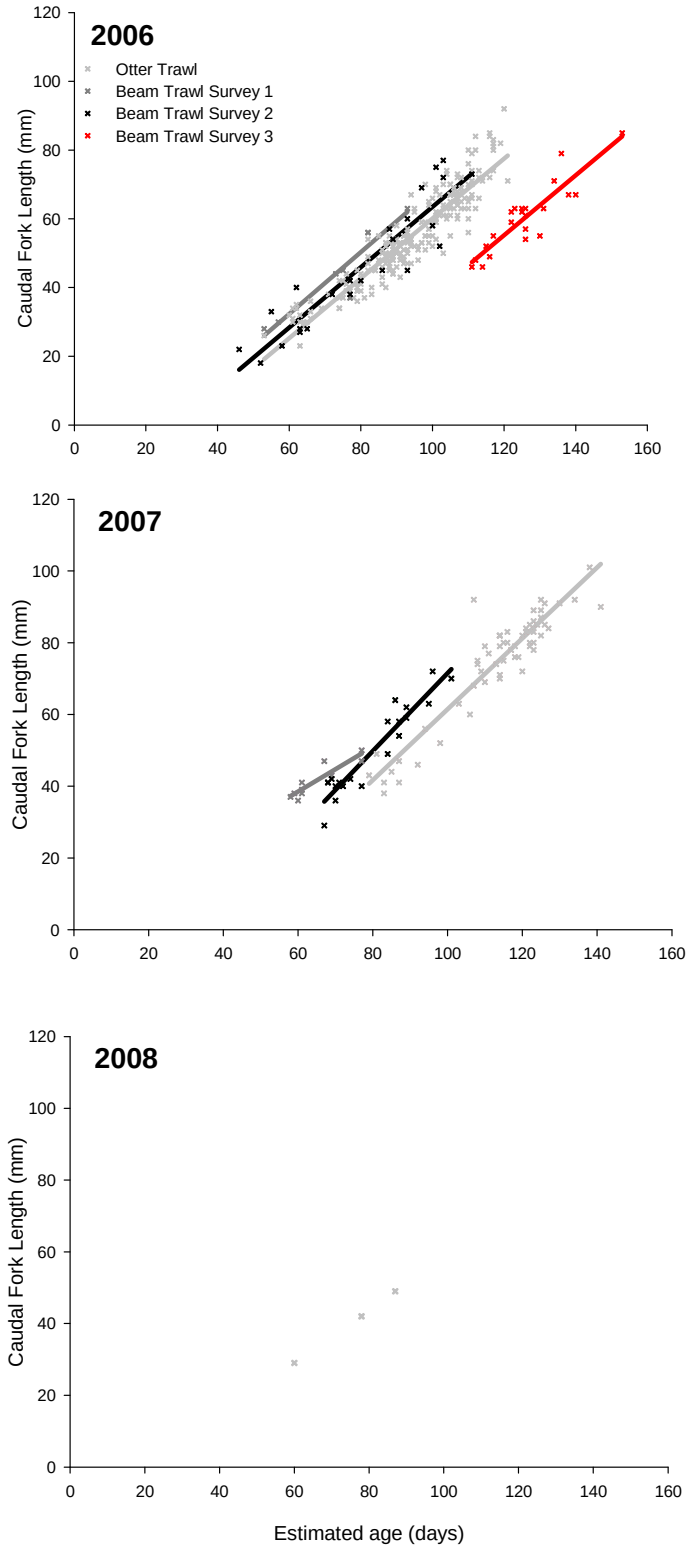


Figure 3.14. Relationship between size and age estimates of 0+ snapper captured on different surveys in each year. Regression lines are shown for each Survey and the regression results are in Table 3.4.

Table 3.4. (a). Results from regression analyses between age and length for samples of 0+ snapper from northern Spencer Gulf for all trawl surveys done in 2006 and 2007 and results of ANCOVA between regression lines for intra-annual comparison. The major points of difference between the regressions are highlighted in bold. (b.) Results from regression analyses between age and length for samples of 0+ snapper from northern Spencer Gulf for the 2006 and 2007 otter trawl surveys, repeated from (a.), with ANCOVA results for inter-annual comparison. (* = significant at 0.05, ** = significant at 0.01, ns = not significant; n.a. indicates that this test was not necessary because the test for slopes was significant).

(a.)

Regressions:							Analysis of covariance:			
Year	Survey	Slope	Intercept	r^2	n	*p*	Factor	df	*F*-ratio	*p*
2006	Beam trawl 1	0.900	-21.725	0.87	8	0.001^{**}	Slope	3,286	0.017	0.997^{ns}
	Beam trawl 2	0.878	-24.310	0.86	24	$<0.001^{**}$	Intercept	3,291	102.915	$<0.001^{**}$
	Otter trawl	0.871	-27.001	0.86	240	$<0.001^{**}$				
	Beam trawl 3	0.871	**-49.306**	0.83	22	$<0.001^{**}$				
2007	Beam trawl 1	0.624	**1.010**	0.84	10	$<0.001^{**}$	Slope	2,83	1.617	0.205^{ns}
	Beam trawl 2	1.086	-37.044	0.89	20	$<0.001^{**}$	Intercept	2,87	15.849	$<0.001^{**}$
	Otter trawl	0.987	-37.257	0.87	59	$<0.001^{**}$				

(b.)

Regressions:							Analysis of covariance:			
Year	Survey	Slope	Intercept	r^2	n	*p*	Factor	df	*F*-ratio	*p*
2006	Otter trawl	0.871	-27.001	0.86	240	$<0.001^{**}$	Slope	1,295	5.124	0.024^{*}
2007	Otter trawl	0.987	-37.257	0.87	59	$<0.001^{**}$	Intercept	n.a.	-	-

Daily somatic growth

The biological intercept method of back calculation was used to provide estimates of daily somatic growth throughout the lives of the 0+ fish and to develop general growth curves. Back calculation was justified because there was a significant relationship between otolith size and caudal fork length (Fig. 3.15). The back-calculated estimates of size at age made it possible to compare growth of fish spawned at different times during the spawning season and to investigate the effect of temperature on growth at a fine temporal scale.

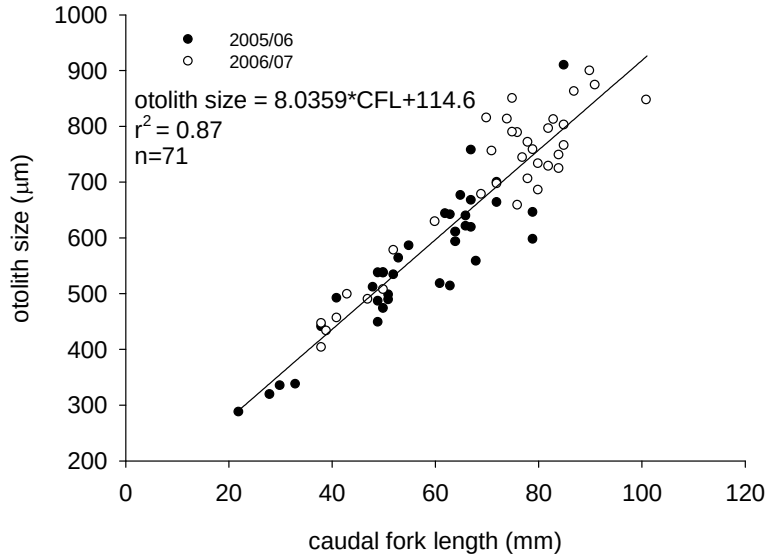


Figure 3.15. Results of regression analyses between estimates of otolith size and caudal fork length (CLF) in each year.

To investigate the effect of spawning time on growth, five fish spawned early, in the middle of, and late in the season, were selected for each year (Table 3.2). Daily somatic growth rate (DSG) increased rapidly for the "early" spawned fish in 2006 for the first 30 days after spawning (Fig. 3.16a). The maximum DSG of 1.13 mm.d^{-1} corresponded with the highest daily average water temperature (25.2ºC). DSG slowed considerably over the next 14 days to 0.65 mm.d^{-1}, corresponding with a decline in water temperature from 25.2ºC to 22.5ºC. Daily somatic growth rate then tracked closely with changes in average daily water temperature until capture. "Middle" spawned fish showed a similar early rapid increase in DSG for the first 30 days. These fish were also exposed to the highest daily average water temperatures observed but at an earlier stage in their life history and their growth rates were lower. The maximum growth rate attained by these fish occurred after the peak in water temperature and was 0.78 mm.d^{-1} when the water temperature was 23.7ºC. DSG then tracked closely with changes in water temperature. "Late" spawned fish followed the same pattern reaching a maximum DSG of 0.80 mm.d^{-1} when the water temperature was at 23ºC. In mid-March, DSG for all groups had converged and tracked very closely with changes in daily average water temperature. DSG and temperature both declined to minima of 0.2 mm.d^{-1} at 17.4ºC in May 2005/06, i.e. the day prior to capture. A significant cross-correlation between daily average water temperature and DSG was observed for each group (Table 3.5).

The general pattern of DSG was similar in 2007 but the maximum for "early" spawned fish was marginally lower than the previous season at 1.09 mm.d^{-1} (Fig. 3.16a). In contrast, "middle" spawned fish had a higher DSG than in the previous season at 1.04 mm.d^{-1}. The

"late" spawned fish also had a higher DSG than the previous season at 0.86 $mm.d^{-1}$. All groups reached their maximum DSG approximately 30 days after having been spawned, at identical water temperatures of 23.1ºC. DSG and temperature declined to minima of 0.4 $mm.d^{-1}$ at 21.1ºC in April of 2007, i.e. the day prior to capture. The close relationship between growth and temperature was confirmed by strong, significant cross-correlations between daily average water temperature and DSG for each group (Table 3.5).

Growth trajectories, i.e. the cumulative sum of DSG, illustrate the effect of DSG and spawning time on final fish length (Fig. 3.16b). Early-spawned fish were 15 mm longer than mid-spawned fish and 25 mm longer than late-spawned fish by early April 2006. In 2007, early-spawned fish were 15 mm longer than mid-spawned fish and 32 mm longer than late spawned fish, at the time of capture, in early April (Fig. 3.16b). When directly compared by fish age (Fig. 3.17), the growth trajectories between years and time of spawning are similar for the first 20 days, begin to diverge from that age and by age 50 days, diverge considerably. This results in the earlier spawned fish being larger for the same age than later spawned fish. There were also differences in the growth trajectories between years, with the early and middle spawned fish from 2007 being larger for their age than any groups from the previous year (Fig. 3.17).

No clear relationship between water temperature and pre-settlement DSG could be determined for either season (Fig. 3.18; Table 3.6). In 2005/06, the post-settlement relationship was clearly exponential and linear regression analysis of the natural log transformed DSG and temperature was significant (Fig. 18; Table 3.6). In 2006/07, the relationship was less clear, but remained significant (Fig. 3.18; Table 3.6). Analysis of covariance indicated that the relationships between post-settlement DSG and temperature differed between years (Table 3.6).

Table 3.5. Cross-correlation coefficient at Lag 0 between average daily water temperature and average daily somatic growth rate for fish spawned at different times during 2005/06 and 2006/07. * indicates a significant cross-correlation where the 95% confidence intervals were breached.

Season	Group	95% confidence intervals	CCF
2005/06	Early	0.192	0.735*
	Middle	0.180	0.613*
	Late	0.191	0.548*
2006/07	Early	0.181	0.744*
	Middle	0.192	0.667*
	Late	0.209	0.405*

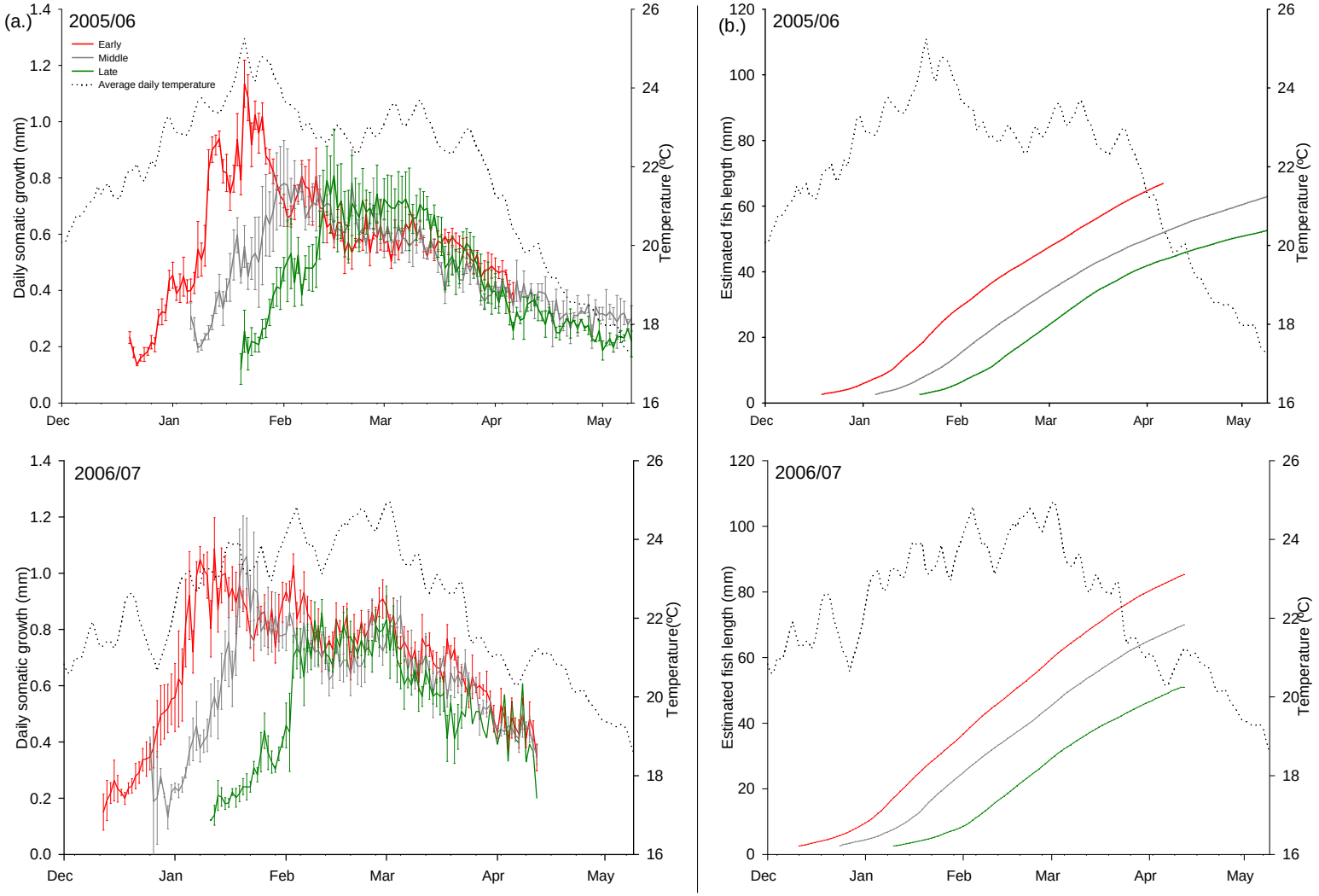


Figure 3.16. (a.) Trajectories of estimates of somatic growth increments derived by back calculation from measurements of daily increments in otoliths for 2005/06 and 2006/07 seasons. Means (± s.e.) are derived from five fish that were spawned early, mid and late in each season. Temperature is daily average logged at Western Shoal. (b.) Estimated growth curves for early, mid and late fish for each year by date.

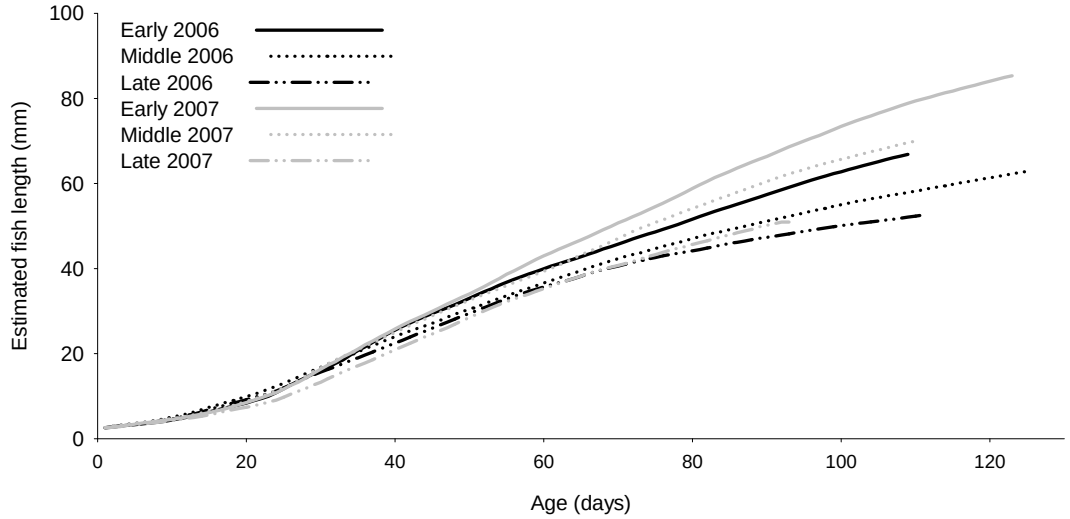


Figure 3.17. Estimated growth curve for early, middle and late spawned fish for each year by age.

Table 3.6. Results of linear regression analyses for pre- and post-settlement somatic growth of 0+ snapper and daily average temperature at Western Shoal for the 2005/06 and 2006/07 seasons. (* = significant at 0.05, ** = significant at 0.01, ns = not significant, n.a. indicates that this test was not necessary because the test for slopes was significant).

Regressions:							Analysis of covariance:			
Year	Survey	Slope	Intercept	r^2	n	*p*	Factor	df	*F*-ratio	*p*
Pre-settlement (1st 25 days of growth)	2006	0.131	-4.113	0.08	69	0.020 *	-	-	-	-
	2007	-	-	-	69	0.224 ns	-	-	-	-
Post-settlement (after day 25)	2006	0.172	-4.450	0.82	341	<0.000**	Slope	1,523	5.717	0.017*
	2007	0.149	-3.792	0.60	186	<0.000**	Intercept	n.a.	-	-

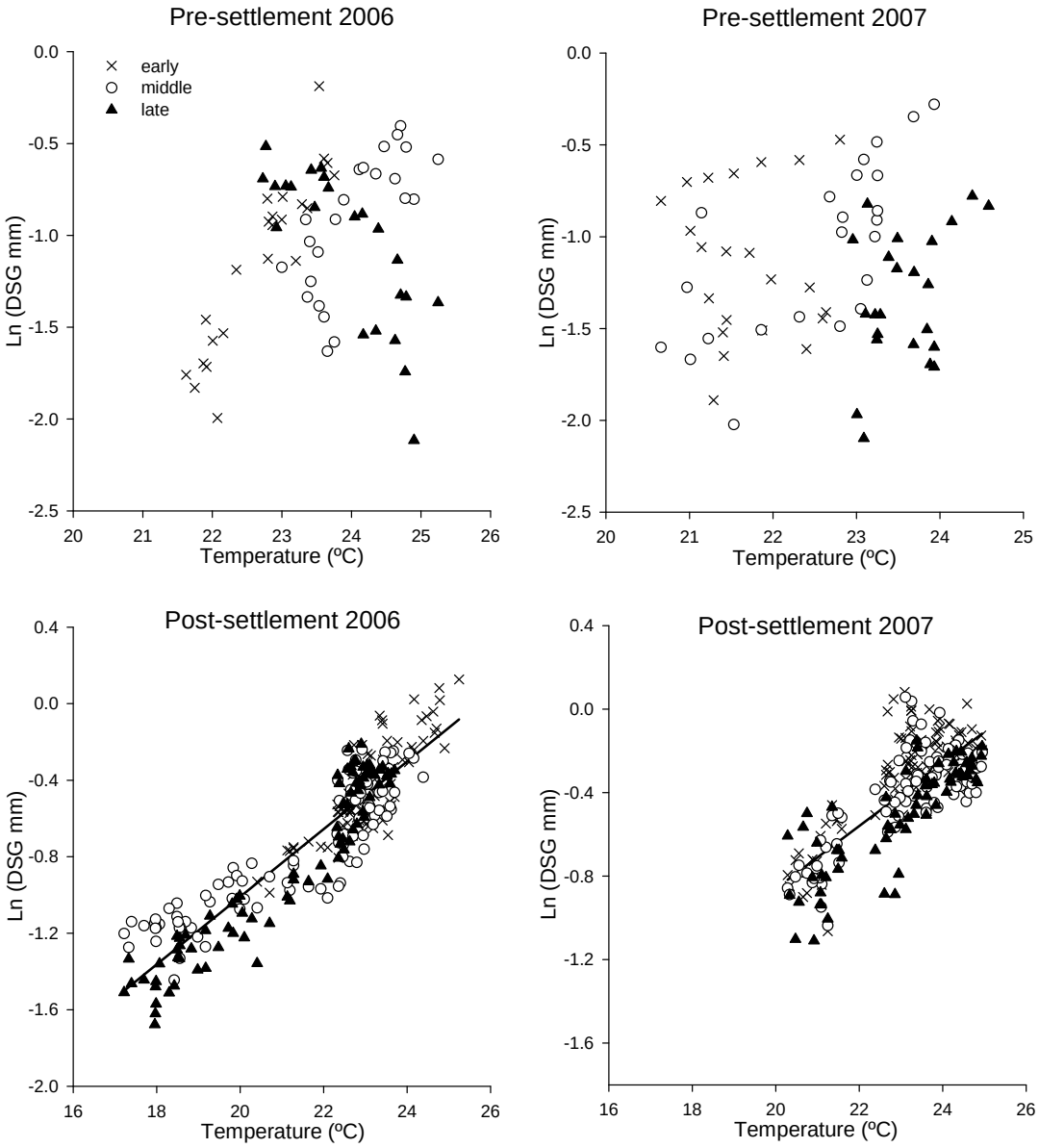


Figure 3.18. Plots of the relationships between temperature and the natural log of daily growth for 0+ snapper captured in 2006 and 2007. DSG estimates were derived from means of five fish that were spawned early, mid and late in each season. Results of the regressions are in Table 3.6.

3.4 Discussion

3.4.1 Distribution

The otter trawl sampling has identified three areas in northern Spencer Gulf that consistently harbour 0+ snapper. This pattern of distribution was identified in the first three years of the otter trawl sampling (Fowler and Jennings 2003) and has remained consistent for the duration of the study. The area adjacent to and immediately to the south of Western Shoal appears to be particularly significant as it produced the highest catch rates from both types of net throughout the study. The area of suitable habitat extended from the drop-off of the seagrass bank on the western shore of the gulf, to the east, a distance of approximately 8 km. The northern limit of the region is just south of the Western Shoal light and its southern limit is about 15 km further south. This is an area that covers a broad depth range from 8 to 24 metres and is characterised by a flat fine mud substratum (Fowler and Jennings 2003). Given that it is an area of approximately 120 km^2 and that densities of ~ 1 snapper per 100 m^2 were observed in 2006 this multiplies up to a population of over one million recruits in that area in 2006.

The beam-trawl identified one other area that may be important near Ward Spit. In this area, the highest densities of 0+ snapper outside of Western Shoal were observed using the beam trawl, but the result was not reflected in the adjacent otter trawl stations. The beam trawl stations were inshore of the otter trawls, i.e. in areas difficult for the larger research vessel to access. The bottom type was complex with trawl by-catch containing numerous large bivalves such as razor fish (*Pinna bicolor*) and hammer oysters (*Malleus meridianus*) (Saunders pers. obs), which contrasts significantly with the fine muddy substratum observed at Western Shoal (Fowler and Jennings 2003). This indicates that a multi-gear approach is of some value for sampling areas that support different habitat types.

The distributions of the 0+ fish observed in the otter trawl sampling were clumped; stations with zero catches were generally adjacent to each other and stations where 0+ snapper were caught were generally adjacent to each other. This clumped distribution pattern was also apparent in the results of the beam trawl sampling. The clumped distribution pattern may result from an association with particular habitat types. In fact, the consistently high abundances at Western Shoal also correlate with the distribution of fine sediments in northern Spencer Gulf (Fowler and Jennings 2003). The observations made at Ward Spit, however, suggested an association with a more complex habitat. It is possible that when 0+ abundances are extremely high the distribution will expand to other habitats, such as at Ward Spit in 2006.

In New Zealand, 0+ snapper occurred with soft sediment (Francis 1995); they have also been found in association with coralline turfing algae on rocky reef (Kingett and Choat 1981). A recent New Zealand study has suggested that the abundance of 0+ snapper over sandy habitat is highest when adjacent to a more complex habitat (Ross *et al.* 2007). In Moreton Bay, Queensland, 0+ snapper were found in association with soft and hard corals, sand, mud and seagrass (Sumpton and Jackson 2005). In Victoria, collections have been made in both shallow water (<4 m) over seagrass (*Heterozostera* sp.) and in deeper (~10 m) muddy habitats (Hamer and Jenkins 2004). It is clear that habitat use by 0+ snapper is flexible but the clumped distribution is a common characteristic throughout their range and is not a simple relationship to a particular habitat type.

The association between 0+ snapper and bare, flat muddy substrate at Western Shoal may result from a high rate of larval supply, a low predation rate, high food availability or a favourable combination of these factors. In Japan, food availability was hypothesised to account for the distribution patterns of 0+ snapper (Azeta *et al.* 1980a; Sudo *et al.* 1983; Tanaka 1985). The distribution and abundance patterns of juvenile fish can be affected by food availability and predation (Beck *et al.* 2001). The distribution patterns of young plaice, *Pleuronectes platessa*, are affected by an interaction between food availability and predator abundance (Phil and Van der Veer 1992; Wennhage and Gibson 1998; Wennhage 2002). Furthermore, post-settlement distribution of 0+ *Gadus morhua*, the Atlantic cod, is considered to be a function of habitat-based variation in vulnerability to predation (Tupper and Boutilier 1995), and have also been demonstrated to select more complex habitats (Laurel *et al.* 2003). The structural complexity of habitats is important in mediating mortality for other species and can strongly influence distribution patterns (Juanes 2007). However, given the habitat at Western Shoal, this is an unlikely explanation for the high abundances of snapper that can occur there.

Hydrodynamic processes can also affect larval supply which affects distribution and abundance in some species (Werner *et al.* 1997). In northern Spencer Gulf, the predominance of south-easterly winds in summer may favour transport of eggs and larvae to the western side of the gulf and account for some patterns of distribution. However, there is insufficient information on wind effects on oceanographic conditions in Spencer Gulf to address this hypothesis at present. The supply of snapper larvae to Western Shoal and possible transport mechanisms is an important topic for future research.

3.4.2 Abundance

The otter trawl and beam trawl generally returned similar catch rates of 0+ snapper between years. As such, the beam trawl net has validated the results from the otter trawl and indicated that it was an effective sampling tool. The catch rates from the beam trawl were, however, too low to estimate annual abundance of 0+ snapper (and therefore recruitment) with confidence. For this, the results from the otter trawl are more informative.

The variation in abundance observed in the otter trawls for the first three years of the trawl survey (Fowler and Jennings 2003) appears to be typical of the region and was consistent with findings of previous studies in Japan (Azeta *et al.* 1980a) and New Zealand (Francis 1995), which demonstrated inter-annual variation of 7 to 20 times. However, in the recent years of this study, the catches demonstrated an inter-annual variation that is an order of magnitude greater than that observed elsewhere. The maximum inter-annual variation was over 200 times, reflecting the apparent near total recruitment failure in 2005 to a record catch the following year. The earliest year-classes (2000-2003) have begun to recruit into the fishery, however, it is too early to assess their importance based on relative contribution to the age distribution of the commercial catch.

Whilst abundances of 0+ snapper have varied considerably over the last nine years, the densities of snapper, even at their maximum, are still quite low (maximum density ~1.4 fish per $100m^2$) but, nevertheless, similar to results of other studies of 0+ snapper (e.g. Hamer and Jenkins 2004). It remains possible that a particularly strong year-class, such as those that occurred in 1991 and 1997 (Fowler *et al.* 2007), would result in higher abundances and wider distributions than observed in this study.

The catch of 0+ snapper was greater during the later beam trawl surveys than the earlier ones. The 1st beam trawl survey in both years was done early in the settlement season and it is possible that not all fish had completed their larval life and were thus not vulnerable to capture. The youngest fish captured during the first surveys was 53 days old (28 mm CFL), and the youngest fish captured in any survey was 43 days old (22 mm CFL). That no 0+ snapper were caught immediately after settlement (i.e. between ~25 and 40 days old) (Fowler and Jennings 2003) suggests that the trawl nets are either not effective at catching the smallest 0+ snapper or that these fish are not present in these areas at this early stage. Back-calculated somatic growth rates indicated that a fish of such an age should be approximately 15 to 20 mm CFL. Given the fine mesh (3 mm^2 aperture knotless mesh in the cod-end, 4 mm^2 body) and that the net captured numerous other species at this size, it seems unlikely that small 0+ snapper are not vulnerable to capture.

3.4.3 Growth

The age-length regressions provided insight into the patterns of growth of snapper through their early life history. Instantaneous growth rate (slope of the regression) did not vary between sampling times, however, the intercept of the regressions increased the later the Survey was conducted. The change in intercept is an indication that there was a considerable slowing of growth with age which was most evident from the beam trawl Survey of May 2006 when fish were considerably older but of a similar size to those fish captured in April.

The process of back calculation from the trajectories of increment widths across otoliths provided a more refined temporal description of growth. Growth increased rapidly to the highest rate soon after settlement, a pattern that was consistent amongst fish spawned at different times. The convergence of the daily somatic growth in the three groups (early, mid and late) suggests that the effect of fish age on growth rate is temporary and that environmental factors become more important. In fact, the relationship between temperature and daily somatic growth is very close for all groups immediately after settlement but did not differ for the pre-settlement period for 0+ snapper collected in 2007, and was only marginally significant for those collected in 2006. When the relationship between pre-settlement period and temperature was considered according to spawning time, significant regressions were derived and one was particularly obvious for the early group in 2006. The relationships differed dramatically for the other groups, however, and are considered spurious. In contrast, the post-settlement relationships between growth and temperature were very similar for all groups as indicated by the regression and cross-correlation analyses.

That no relationship between water temperature and pre-settlement growth was identified in this study is not consistent with other studies. Temperature impacts growth of larval snapper in aquaculture (Fielder *et al.* 2005) and the length of the larval period in New Zealand (Francis 1994b). A possible explanation for this anomaly is that the temperature data used in the regressions were not representative of the environmental conditions to which the fish were exposed as larvae. It is possible that some of the 0+ snapper caught were spawned in an area that is not represented by the temperature profile at Western Shoal and that they spent a considerable period elsewhere during their early life. There is evidence to support this hypothesis from the abundance data in that no 0+ were captured at an age of less than 40 days, in spite of the temporal intensity of the sampling and the fine mesh gear used during early 2006 and 2007. Furthermore, this study collected "successful" recruits and the effect of temperature may not be one of increased growth rate but rather of survival. In the 2008 sampling season, recruitment was so reduced that insufficient samples of fish were collected

to study growth. In that year, larval snapper may have been spawned at times when they were exposed to lethal temperatures and are consequently not represented in this study of growth. There is, therefore, a need for future research that directly addresses larval abundance and growth patterns.

The timing of spawning had a considerable impact on fish size. Early spawned fish were exposed to conditions conducive to fast growth for longer than fish spawned later in the season and were of a considerably greater size when water temperatures decreased. This result is intuitive and has been previously noted for snapper (Fowler and Jennings 2003). It indicates that fish spawned later in the season do not have the opportunity to catch up with their earlier spawned counterparts. It is likely that fish size is an important determinant of survival with faster growth resulting in lower mortality through predation and enhanced ability to feed (Houde 1987). The timing of spawning can be important for survival. In some species, those spawned earlier in the season are more likely to survive than those spawned later (Cargnelli and Gross 1996; Lapolla and Buckley 2005). In the case of haddock (*Melanogrammus aeglefinus*) this is thought to relate to increased predation later in the season (Lapolla and Buckley 2005), but in the case of the freshwater bluegill (*Lepomis macrochirus*) the early spawned fish are thought to survive better because of a longer growing season prior to their first winter. In other cases, particularly long-term studies, inter-annual variation in the timing of successful spawning is common (Fowler and Jennings 2003; Wright and Gibb 2005; Chapter V).

The growth trajectories also yielded some interesting inter-annual comparisons. No differences were observed for the larval period, but the early and middle spawned fish from 2007 reached larger sizes at an equivalent age than those from 2006. Thus, the year with lower abundances of 0+ snapper had higher post-settlement growth and reached larger sizes for a given age. The result hints at possible density-dependent effects on growth. A similar result has also been obtained for Walleye Pollock (*Theragra chalcogramma*) where faster growth was found for weaker year-classes (Nishimura *et al.* 2007). These results differ again from a study of Atlantic Cod (*Gadus morhua*) where otolith size at age and body-size at age at the pelagic juvenile stages were correlated with year-class strength but not with larval growth (Campana 1996).

The effect of temperature on post-settlement growth and the relationship between spawning time and fish size are both factors that may impact on year-class strength. These are factors that are more likely to determine abundance later in the life history and there are clear differences in the inter-annual patterns of abundance in the very early life history. Thus, the

factors that control the inter-annual pattern of abundance observed in this study may be determined by egg production or survival to age 50 days. A detailed examination of the spawning period, an assessment of which parts of the season are successful, and a consideration of environmental variation during the spawning period may provide a better understanding of the conditions required for the establishment of a strong year-class. These are the subjects of Chapters IV and V.

Chapter IV

The spawning dynamics of snapper, *Chrysophrys auratus*, in northern Spencer Gulf, South Australia: implications for recruitment variability

4.1 Introduction

The causes of annual variation in recruitment of fish have attracted considerable research attention since the phenomenon of variable year-class strength was first observed early last century (Hjort 1914). Among the possible explanations for recruitment variation is that egg production differs between years as a consequence of spawning biomass and/or spawning activity of the population. Spawning biomass can change over time as a consequence of fishing and natural mortality as well as migration but considerable changes in egg production over a shorter time scale may occur through variations in spawning activity. Spawning activity can vary considerably through changes in fecundity, the length of the season and the frequency of spawning events (Hunter *et al.* 1985; DeMartini 1991). These factors may influence the number of potential recruits available to a population even before factors such as mortality through starvation or predation become important.

At extremes, inter-annual variation in reproduction can result in skipped spawning. This occurs when individuals of an annual spawning species do not spawn every year and has been observed for some iteroparous fish, such as *Gadus morhua* (Rideout *et al.* 2005). Changes in reproductive output are considered important when calculating spawning biomass using egg production methods (Alheit 1993; Zeldis and Francis 1998; Somarakis *et al.* 2004) but are rarely considered when accounting for variation in recruitment. Variation in spawning parameters that can affect egg production are thought to relate to abiotic and biotic environmental changes such as temperature and nutrition (DeMartini 1991; Rideout *et al.* 2005).

The reproductive biology of the snapper, *Chrysophrys auratus* (Sparidae) has been studied in several places across its range in regions that offer a broad range of environmental conditions. These studies have identified numerous consistencies in snapper reproductive biology such as iteroparity, multiple batch spawning, asynchronous oocyte development and indeterminate

fecundity (Japan, Matsuyama *et al.* 1991; New Zealand, Scott and Pankhurst 1992; Scott *et al.* 1993). However, differences in reproductive characteristics have also been found. These include the timing of spawning and the associated environmental conditions, such as water temperature and photoperiod in which fish spawn (Japan, Higuchi 1977 in Mihelakakis and Yoshimatsu 1998; New Zealand, Crossland 1977a,b; Scott and Pankhurst 1992; Australia, Ferrell and Sumpton 1998; McGlennon 2003). Such differences highlight the need to understand the reproductive biology of the species at the local scale in order for fisheries to be managed most effectively.

This study investigated the reproductive biology of snapper in northern Spencer Gulf, South Australia. This is a region that, in spite of the species' broad distribution throughout the coastal waters of the State, has in most years accounted for >50% and sometimes as much as 75% of the State's catch, and supports some of the highest densities of snapper in Australia (Fowler *et al.* 2007). The catch in this region depends on the number and relative strength of the different year-classes that comprise the population (McGlennon *et al.* 2000, Fowler *et al.* 2007). Further, variation in year-class strength has been linked to inter-annual variation in the recruitment of 0+ snapper (Fowler and Jennings 2003). Considerable within-season variation in snapper recruitment has also been identified (Fowler and Jennings 2003; Chapter III). This variation in recruitment of 0+ fish may result from variation in reproductive output in response to inter-annual variation in environmental characteristics. To consider such possible effects, knowledge of the temporal dynamics of spawning is essential.

The primary aim of this study was to measure temporal variation in spawning activity and to relate the timing of the spawning season to water temperature. To achieve this several reproductive parameters were determined. First, the hypothesis that snapper are multiple batch spawners with asynchronous oocyte development and indeterminate fecundity was tested. This was done through analysis of the microscopic characteristics of ovaries at different developmental stages and by analysing the organisation of oocytes within the ovary matrix. Spawning activity was then determined by analysing the microscopic characteristics of ovaries to differentiate spawning and non-spawning females. Finally, the effects of fish size on spawning activity and batch fecundity were determined for each spawning season.

4.2 Methods

4.2.1 Water temperature

Water temperature at Western Shoal, in northern Spencer Gulf (Fig. 4.1), was recorded using a temperature data logger (StowAway TidBit™). This was attached to a navigation beacon on 20th September 2005 by divers on SCUBA. It logged temperature hourly over the study period at a depth of ~ 6 m (1 m off the bottom). The logged data were downloaded on November 12th 2006, August 20th 2007 and April 23rd 2008.

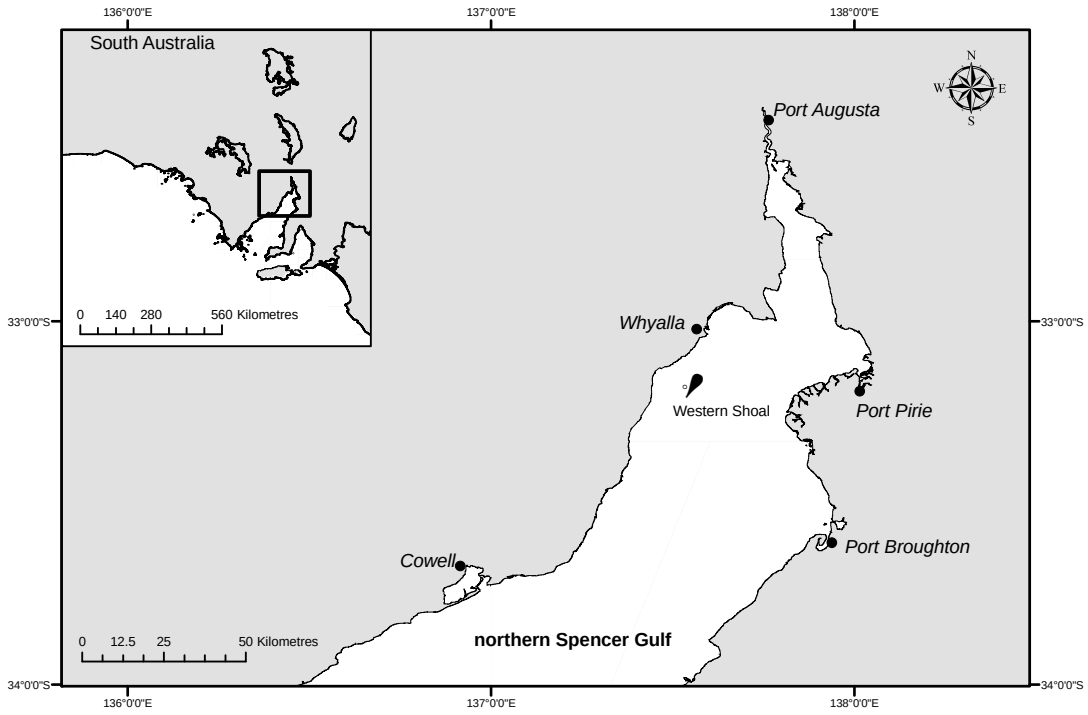


Figure 4.1. Map of northern Spencer Gulf. Major towns are indicated along with navigational beacons where the temperature data logger was deployed. Inset shows the coastline of South Australia highlighting the location of the study region.

4.2.2 Sample collection and processing

Adult fish were collected from three sources: the commercial fishing sector, the charter boat sector and by research sampling. The catch of the commercial marine scale fish fishery was sub-sampled at the SAFCOL fish market, where fish are generally received within 24 hours of their capture. Fish considered likely to have been captured in northern Spencer Gulf (confirmed later from discussions with fishermen or back-tracking through catch returns) were accessed for dissection. Charter boat fishers also provided gonads from snapper that had been processed on board. These gonads were placed in snap-lock plastic bags by the charter operator, put on ice, transported to Adelaide and generally delivered within 24 hours of fish capture. In November 2005, 2006 and 2007 some fishery independent sampling was

undertaken because the fishery was closed during these months. Such sampling was necessarily limited, due to the logistic constraints and the expense of such collections.

In total, 1556 fish were collected between September 2005 and January 2008 inclusive from northern Spencer Gulf (Fig. 4.1). Although sampling effort varied considerably throughout the study, some fish were collected in most months (Table 4.1). Sampling effort was concentrated in December and January of each year when samples were collected as often as possible in order to describe the fine-scale temporal dynamics of spawning.

Table 4.1. Summary of samples collected from northern Spencer Gulf during the study. M, market samples; Ch, Charter fisher samples; FI, Fishery independent samples.

Month	Number of samples	Number of females	Number of males	Total	Sample classification
Sep-05	1	3	6	9	M
Oct-05	11	70	56	126	M, Ch
Nov-05	1	7	5	12	FI
Dec-05	17	182	177	359	M, Ch, FI
Jan-06	7	48	70	118	M, Ch
Feb-06	4	20	15	35	M, Ch
Mar-06	1	10	6	16	M
Jun-06	2	4	5	9	M
Aug-06	1	2	2	4	M
Sep-06	1	17	8	25	M
Oct-06	2	18	11	29	M
Nov-06	2	19	26	45	FI
Dec-06	13	149	110	259	M, Ch
Jan-07	8	54	55	109	M, Ch
Feb-07	1	4	3	7	Ch
Mar-07	1	4	5	9	Ch
May-07	1	6	6	12	M
Jul-07	2	35	16	51	M
Aug-07	4	15	16	31	M
Sept-07	1	16	8	24	M
Oct-07	2	20	26	46	M
Nov-07	2	25	42	67	M, FI
Dec-07	6	54	44	98	M
Jan-08	5	29	27	56	M

Fish from market samples and research trips were measured for caudal fork length (CFL) from the tip of the snout to the posterior end of the middle caudal rays to the nearest mm and weighed to the nearest 10 g. The gonads were removed, sexed and weighed to the nearest 0.1 g. Gonadosomatic indices (GSI) were calculated as GSI = $[W_g/W_f]*100$, where W_g is gonad weight and W_f is gonad-free fish weight. No information was available on fish length and weight for samples from the charter boat sector so GSI values could not be calculated for those fish. Cross-correlation analysis between male and female GSI was used to test the synchronicity of gonad development between the sexes.

For all samples, ovaries were classified macroscopically to one of five stages of development based on size, colour and visibility of oocytes (Table 4.2). Testes were examined macroscopically and were classified to one of three stages of development (Table 4.2).

4.2.3 Laboratory analysis of preserved samples

All ovaries at Stages 3, 4 and 5 and some Stage 1 and 2 ovaries were subjected to more detailed analysis by histological preparation and microscopic examination. For such ovaries (n=594) a segment was removed from the centre of one lobe and preserved in formalin. Histological sections were prepared from the formalin-preserved tissue for microscopic analysis. Tissue was sectioned at 6 µm and stained with haematoxylin and eosin. The slides were examined using a compound microscope at 100x magnification. Based on the microscopic examination of these slides, fish were classified into two groups: mature spawning and mature non-spawning. Mature spawning fish were defined as those with ovaries that contained oocytes that were at the migratory nucleus stage or were hydrated, or those with ovaries that contained new post-ovulatory follicles (equivalent to Stage 1 POFs defined in Matsuyama *et al.* 1988). Mature, non-spawning fish were defined as those mature fish with ovaries that lacked any features that suggested spawning was imminent or had occurred recently.

4.2.4 Spawning mode

To determine the spawning mode, oocyte frequency distributions were calculated from histological slides from two fish that had been classified to Stage 3 according to the criteria in Table 4.2. Oocytes were classified as either unyolked, yolked or advanced yolked according to the criteria in Table 4.3. Oocytes were measured using a compound microscope at 100x magnification using Optimas™ image analysis software. For each section all oocytes for which the nucleus was visible were measured for maximum diameter from six 1300 by 1600 µm non-overlapping frames.

Table 4.2. Stages of development of ovaries and testes of *Chrysophrys auratus.*

Sex	Macroscopic Stage	Macroscopic description
Female	Stage 1 (Immature)	Sexes almost indistinguishable, ovaries narrow threads, colour variable.
	Stage 2 (Developing/resting)	Ovaries small, opaque, pink in colour, no oocytes visible.
	Stage 3 (Ripe)	Ovaries medium to large, orange or yellow in colour, large oocytes easily visible but not translucent.
	Stage 4 (Gravid/running ripe)	Ovaries large, orange or yellow and speckled with large translucent oocytes. Oocytes may be ovulated.
	Stage 5 (Spent/resting)	Ovaries flaccid, medium to small in size, generally red, particularly at posterior end, with some remnant oocytes visible.
Male	Stage 1 (Immature)	Sexes almost indistinguishable, testes narrow threads, colour variable but usually cream.
	Stage 2 (Developing/resting)	Testes small to medium, white in colour, no milt visible when gonad cut.
	Stage 3 (Ripe)	Testes large, creamy white, milt easily visible when gonad cut.

A frequency distribution of whole oocyte diameters was also calculated for two fish with Stage 4 ovaries. A large section (40 g) was removed from the centre of one ovary from each fish and preserved in 5% formalin. At a later date, this material was homogenised and a sample of 2 mL was pipetted out and placed in an egg counting tray. Whole oocyte diameters were then measured using a dissecting microscope at 20x magnification using Optimas™ image analysis software.

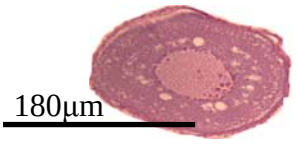
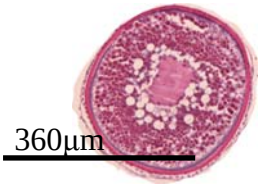
4.2.5 Spawning fraction and spawning frequency

The estimates of spawning fraction reflect the proportion of mature females that were classified as spawning and were estimated using the formula $S_f = N_{fs}/N_{fm}$ where S_f = spawning fraction, N_{fs} = the total number of spawning females and N_{fm} = the total number of mature females in the sample. Spawning frequency (S_{fq}) estimates were also calculated as $S_{fq} = 1/S_f$ and provided an estimate of the average interval between spawning events in days. This was only done for samples of fish that contained six or more mature females.

Spawning fraction and frequency estimates were calculated for different size classes of fish, using the same conventions defined above, for all samples that contained mature females from the month of December each year. Size classes were considered in three 200 mm length classes (301-500 mm, 501-700 mm and > 701 mm CFL). To test whether spawning frequency differed between size classes, a chi-squared contingency test was done on the numbers of spawning and non-spawning females in each size class for the fish collected during December 2005. This was the only period with suitable numbers of fish from each size class.

To determine the temporal variation in spawning activity, spawning fraction and frequency estimates were calculated on a fortnightly basis for the period from November 14th until January 31st for each of the three seasons. The peak in spawning activity occurred in December each year and this period was used to compare the relative frequency of spawning and non-spawning females between years using a chi-squared contingency test.

Table 4.3. Descriptions of different oocyte classifications used in size frequency distributions calculated from histological slides from Stage 3 ovaries. Descriptions are adapted from Matsuyama *et al.* (1988).

Oocyte stage	Description	Image
Unyolked	Smallest oocytes stain heavily with haematoxylin with large nucleus containing several nucleoli	
Yolked	Generally larger than unyolked oocytes. Lipid granules throughout cytoplasm. Zona radiata thin.	
Advanced yolked	Wide eosinophilic zona radiata. Eosinophilic yolk proteins throughout cytoplasm	

4.2.6 Batch fecundity

Batch fecundity estimates were made for ovaries that were classified macroscopically as Stage 4 (Table 4.2). For these ovaries, a sub-section of approximately 10% by weight was dissected from one lobe of the ovary and weighed to the nearest 0.01 g. This was split and the oocytes washed from the ovary matrix, collected in a 500 µm filter, transferred to a 1 L jar and preserved in 5% formalin. At a later date, these samples were rinsed in a 150 µm filter to remove the preservative, after which the oocytes were placed in water, making the volume up to 1 L. This 1 L sample was agitated to distribute the oocytes evenly. Then ten 1 mL sub-samples were taken and examined under a binocular microscope using transmitted light. For each sub-sample, hydrated oocytes (>700 µm) were counted. The average number of hydrated oocytes per mL was then calculated. The final estimate of batch fecundity was made by calculating the average number of hydrated oocytes per mL to the full sample volume and the combined weight of both ovaries using the formula: $B_f = [(\overline{x}_{sub}*1000)/W_{sect}]*W_O$ where B_f = batch fecundity, $\overline{x}_{sub}$ = average count of hydrated oocytes in the 1 mL sub-samples, W_{sect} = weight of the sub-section and W_O = the whole weight of the ovaries.

4.3 Results

4.3.1 Temperature

The lowest temperatures were below 12ºC during July of each year and reached maxima over 25ºC in late February in 2005/06 and early March in 2006/07. The highest daily averages were over 24ºC. Daily temperature fluctuations at Western Shoal were considerable, reaching a maximum of 2.7ºC, but was most commonly less than 1ºC (Fig. 4.2).

The rate of temperature rise during late spring and early summer was similar in 2005 and 2006, reaching 20ºC on the 23rd and 28th of November, respectively (Fig. 4.2). In 2005/06 this was followed by a period of gradually increasing daily temperature which reached a peak on January the 22nd at 25.2ºC, after which temperature dropped gradually to 22.3ºC until mid-February, recovering to 23.7ºC by mid-March. Temperatures then dropped until July. The following season differed markedly in two ways. There was a period in December when water temperature dropped dramatically by 2ºC before increasing again but at a slower rate than in the previous season. In this season the maximum water temperature was not reached until the 1st of March (Fig. 4.2), after which, temperatures dropped consistently until July (Fig. 4.2). In November 2007 water temperature rose more rapidly than during the same month in the two previous years, reaching 20ºC on the 16th November (Fig. 4.2). After this, the rate of rise slowed considerably and there were some short periods during which

temperature dropped. Water temperature reached 24.2ºC on 2nd January and remained at or around 24ºC for longer than the two previous years and did not begin to decline until the 4th February 2008. This was followed by several fluctuations during which temperature dropped several degrees and then recovered to around 24ºC. The maximum water temperature reached was 24.5ºC on the 17th March 2008, which occurred at the end of an unusual period of extremely hot weather conditions during which daily maximum air temperatures at Whyalla exceeded 35ºC for 15 days running (Bureau of Meteorology 2008).

4.3.2 Microscopic characteristics of ovaries at different stages of development

Stage 1 (immature) ovaries were rarely collected in this study as the samples were primarily collected from commercial catches which are subject to a minimum legal size of 38 cm total length. Immature ovaries were characterised by a tight arrangement of unyolked oocytes. Stage 2 (developing/resting) ovaries had both yolked and unyolked oocytes also packed tightly with few gaps in the ovary matrix (Fig. 4.3). No atresia was present in either Stage 1 or 2 ovaries.

Stage 3 (ripe) ovaries always contained some unyolked oocytes as well as some partially yolked oocytes, but were characterised by the presence of some advanced yolked oocytes (Fig. 4.3). Occasionally some oocytes with migratory nuclei were present indicating that spawning was imminent for these fish. Some Stage 3 ovaries also had post-ovulatory follicles indicating spawning had occurred recently. The ovary matrix was more open than for Stages 1 and 2 and a few atretic oocytes were sometimes present.

Stage 4 (gravid/running ripe) ovaries were characterised by the presence of hydrated oocytes but they also had unyolked, partially yolked and advanced yolked oocytes (Fig. 4.3). Some Stage 4 ovaries also had migratory nucleus oocytes or post-ovulatory follicles. The ovary matrix was generally loose and hydrated oocytes were often distorted. Some minor atresia was often evident.

Stage 5 (spent) ovaries were characterised by a high incidence of atresia (Fig. 4.3). They also had unyolked, partially yolked and advanced yolked oocytes and, rarely, migratory nuclei oocytes. Post-ovulatory follicles and hydrated oocytes were not found in these ovaries.

4.3.3 Spawning mode

Oocytes at a range of developmental stages and post ovulatory follicles at different stages of degeneration co-occurred in ovaries of mature spawning and mature non-spawning fish. Unyolked oocytes measured 27 to 157 μm, overlapping in diameter with small yolked oocytes, which in turn ranged in size from 116 to 332 μm (Fig. 4.4). Advanced yolked oocytes also showed a considerable range in size, from 248 to 491 μm, overlapping in size with yolked oocytes (Fig. 4.4). The size distributions were continuous across the developmental stages.

The size distributions of formalin-preserved whole oocytes were clearly bimodal, with the two modes relating to hydrating and non-hydrated oocytes (Fig. 4.5). The size distributions of oocytes that were non-hydrated were continuous and showed no clear gaps or modes. Since all these oocytes were opaque it was not possible to differentiate them into the unyolked, yolked and advanced yolked stages. Hydrating oocytes ranged in size from 705 to 1080 μm with a mean at 830 μm.

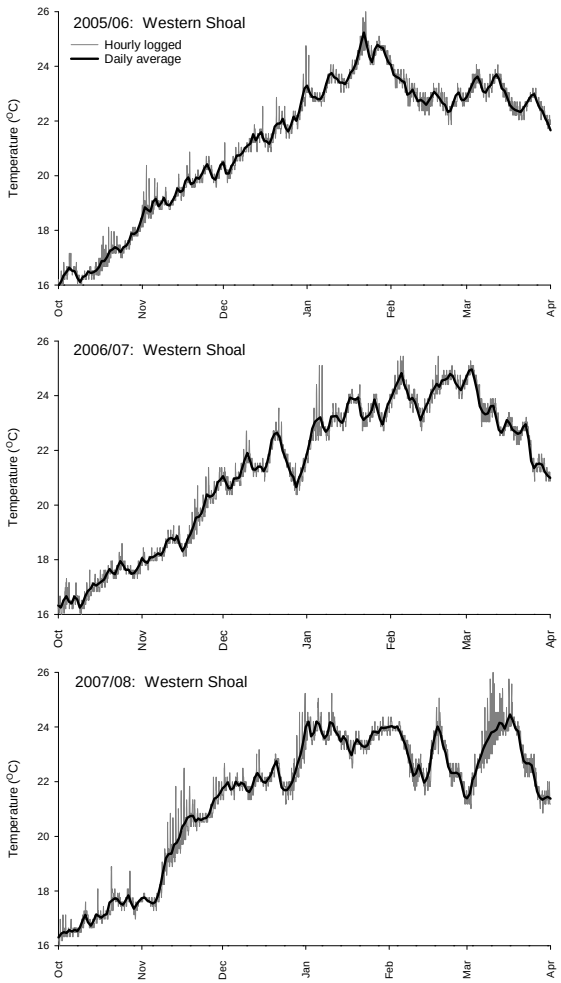


Figure 4.2. Hourly logged water temperature data overlaid on the daily average water temperature at Western Shoal for 1st of October to 1st April for the three seasons.

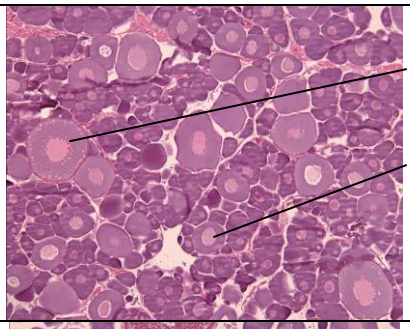
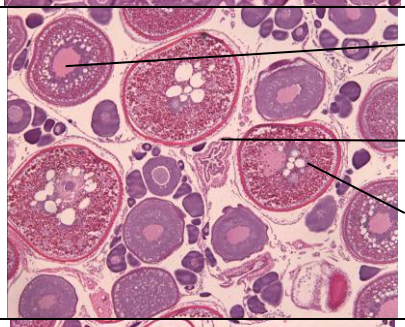
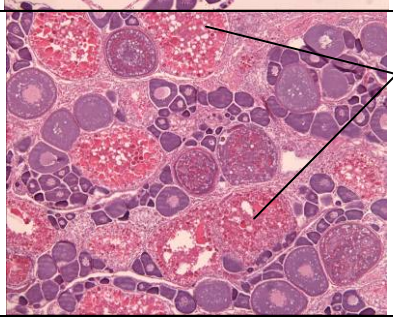
Macroscopic stage and histological characteristics	Section(1300 x 1600 μm)
Stage 2 (Developing/resting) Mostly unyolked oocytes with some partially yolked	
Stage 3 (Ripe) Unyolked, partially yolked and advanced yolked oocytes present. Occasionally some post-ovulatory follicles and minor atresia present.	
Stage 4 (Gravid/running ripe) All oocyte stages present. Some post-ovulatory follicles may be present but generally dominated by advanced yolked and hydrated oocytes.	
Stage 5 (Spent/resting) Oocytes of all stages may be present but atresia is advanced. Post-ovulatory follicles not found.	

Figure 4.3. Descriptions and digital images of microscopic characteristics of different mature ovary stages. H = hydrated, Uy = unyolked, Py = partially yolked, Ay = Advanced yolked, Mn = Migratory nucleus, POF = post-ovulatory follicle.

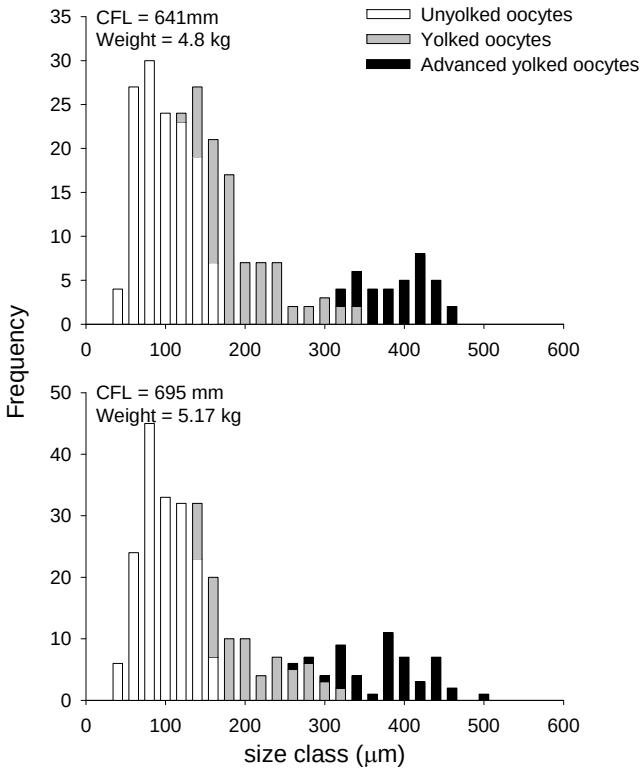


Figure 4.4. Size frequency distributions of oocytes from histological slides of two Stage 3 ovaries. Shown are CFl and weight of each fish.

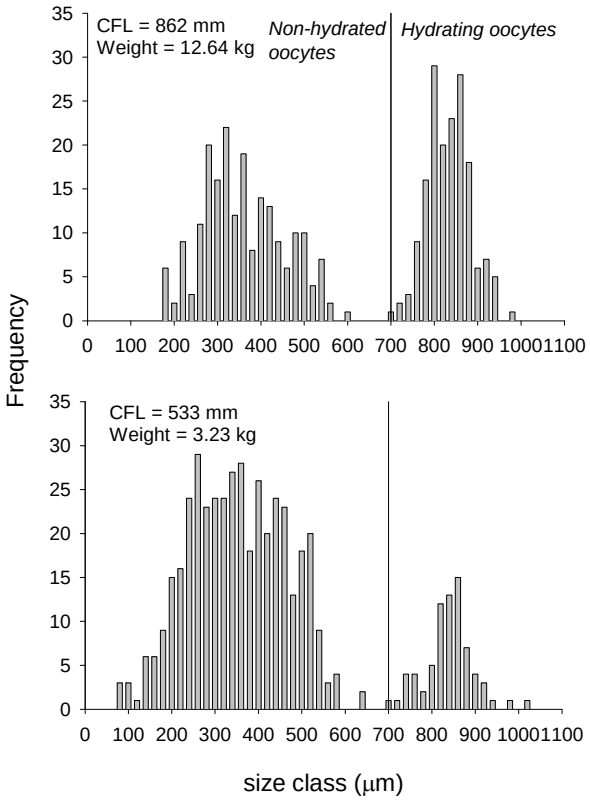


Figure 4.5. Size frequency distributions of whole oocytes for two Stage 4 ovaries. Shown are CFL and weight for each fish.

4.3.4 Timing and extent of spawning season

Gonadosomatic indices. Variation in GSI for females indicated that the main period of gonad development was from November to January, with a peak in December. In 2005, GSI increased from September, peaked in December at 4.0% and then decreased through January and February dropping to 0.5% in March 2006 (Fig. 4.6a). GSI then remained low until increases were recorded in October 2006, peaking in December before decreasing rapidly again to low levels of <1.0% in March 2007, remaining low until November 2007. The peak in GSI for the 3rd season was also in December at approximately 4%. In this final season, however, GSI decreased earlier, averaging approximately 1% in late January.

In the first two seasons the initial rise in GSI occurred in October with average temperatures of 16.9 and 17.1ºC (Fig. 4.6). This initial rise was not observed in October 2007 even though water temperatures were very similar (17.1ºC). GSI had reached levels similar by November each year when average temperatures were 19.5, 19.1 and 19.7ºC, respectively. The peak in GSI occurred in December each season when average temperatures were 21.4, 21.4 and 22.1ºC, respectively. GSI was lower in January in all years, dropping whilst temperatures continued to rise, or at least remained high (Fig. 4.6).

The pattern of GSI observed in males and females was similar and cross-correlation analysis was significant at lag 0 (CCF_{lag0} = 0.983, 95% C.I. = 0.3714), indicating strong temporal synchronicity in gonad development between the sexes (Fig. 4.6). Variation in male GSI indicated that the main period of gonad development was from November to January, with peaks in November and December. In 2005, GSI increased from October, peaked in December at 4.8% and then decreased to <1.0% in March 2006 (Fig. 4.6b). GSI then remained low until increases were recorded in October 2006, peaking in January before decreasing rapidly again to <1.0% in March 2007. GSI remained low until November 2007. The maximum GSI for this season occurred in December, but was considerably lower than for the two previous seasons. GSI also decreased more rapidly than for the earlier two seasons, averaging only 1% in January 2008.

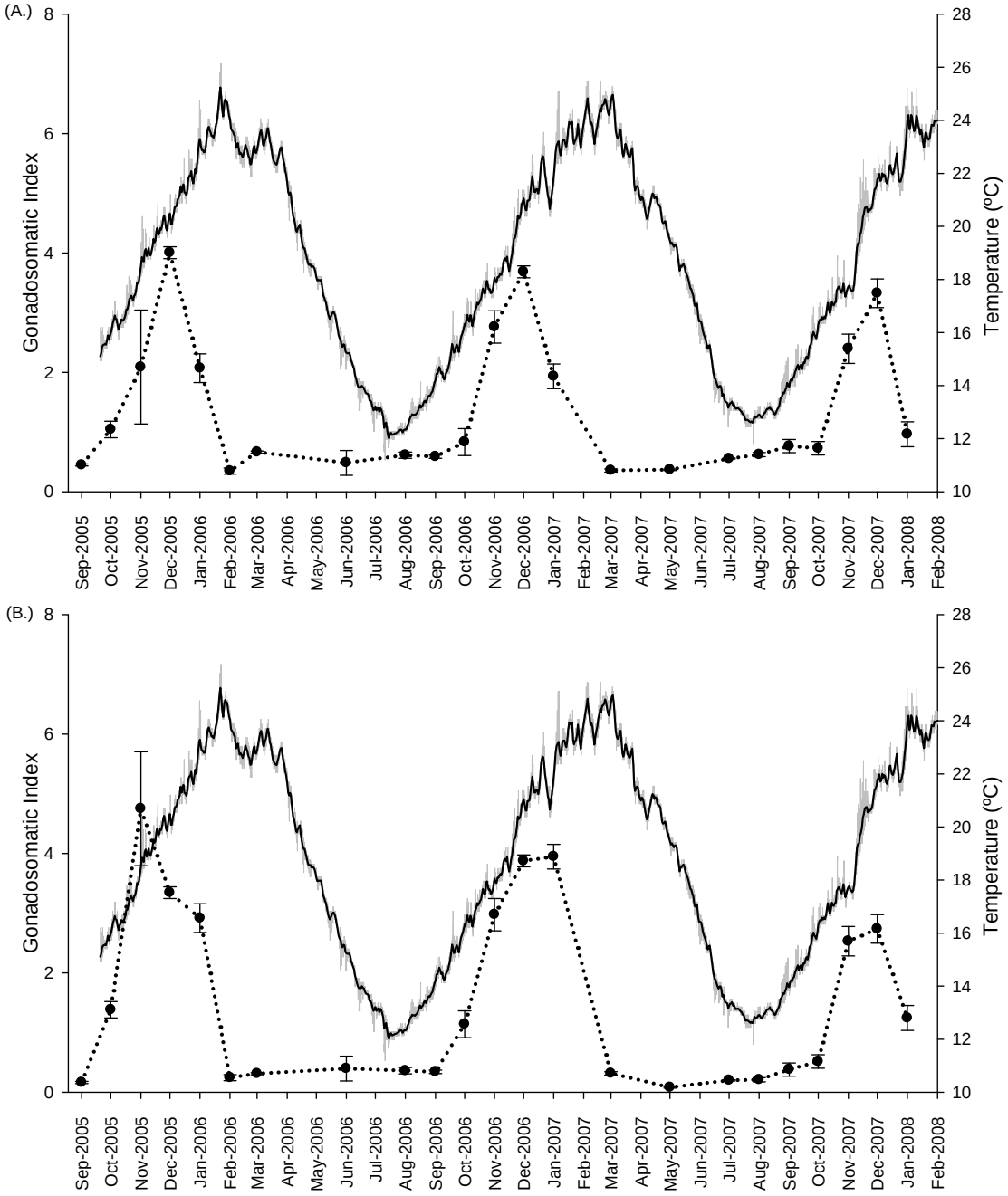


Figure 4.6. Gonadosomatic indices (dotted line) for (A) females and (B) males by month with temperature data overlaid. The grey line is hourly logged temperature data and the black line is daily average temperature logged at Western Shoal. Error bars are standard error.

In September 2005, all mature females had ovaries in a resting state (Stage 2) (Fig. 4.7a). Towards the end of October 2005 the first Stage 3 ovaries were recorded, but in low numbers. In November, Stages 3 and 4 ovaries were present, but the latter were rare. By December, 50% of ovaries were Stage 4, Stage 3 ovaries were common and Stage 2 were rare. In January 2006, all maturity classifications were present but Stage 4 ovaries were less abundant and Stage 5 ovaries were present in samples for the first time. By February, no Stage 4 ovaries were found, those at Stages 2 and 5 dominated; in March 2006, all ovaries were classified at Stage 2. The pattern was similar in both 2006/07 and 2007/08 with the first Stage 3 ovaries recorded in late October, Stage 3 and 4 ovaries dominating during December and becoming rare during January. The only major difference between seasons was the presence of some Stage 5 ovaries during December 2006 and the absence of Stage 4 ovaries in November 2007. Overall, the data indicated from macroscopic staging of ovaries that the spawning season for snapper began during November or early December, peaked in December and had ended in early February.

In September 2005, all mature males had testes in a resting state (Stage 2) (Fig. 4.7b). The first Stage 3 testes were recorded in October, but in low numbers. In November all testes were at Stage 3, whilst by December, all maturity stages were present. In January 2006, all maturity classifications were present. In February, testes were most commonly at Stage 2. In March 2006, all testes were classified at Stage 2. The pattern was nearly identical in the following two seasons, with the only major differences being that in November 2006 and 2007 both Stage 2 and 3 testes were present and in December 2006 only Stage 3 testes were present.

The first Stage 3 ovaries were found when water temperature reached 16.9ºC in October 2005. The first Stage 4 (gravid/running ripe) fish were identified in November 2005 when temperature averaged 19.5ºC. Most Stage 4 fish were identified in December 2005 when water temperature for that month averaged 21.4ºC (range: 19.7ºC to 24.8ºC). In January the first spent fish were identified when temperature was at its highest, with an average of 23.8ºC (range: 22.5 to 26.1ºC). In February, spawning had finished but water temperature was still high, averaging 23.0ºC. The 2006/07 season did not differ substantially. However, in 2007/08 Stage 4 ovaries were not observed until early December when the temperature was 22ºC.

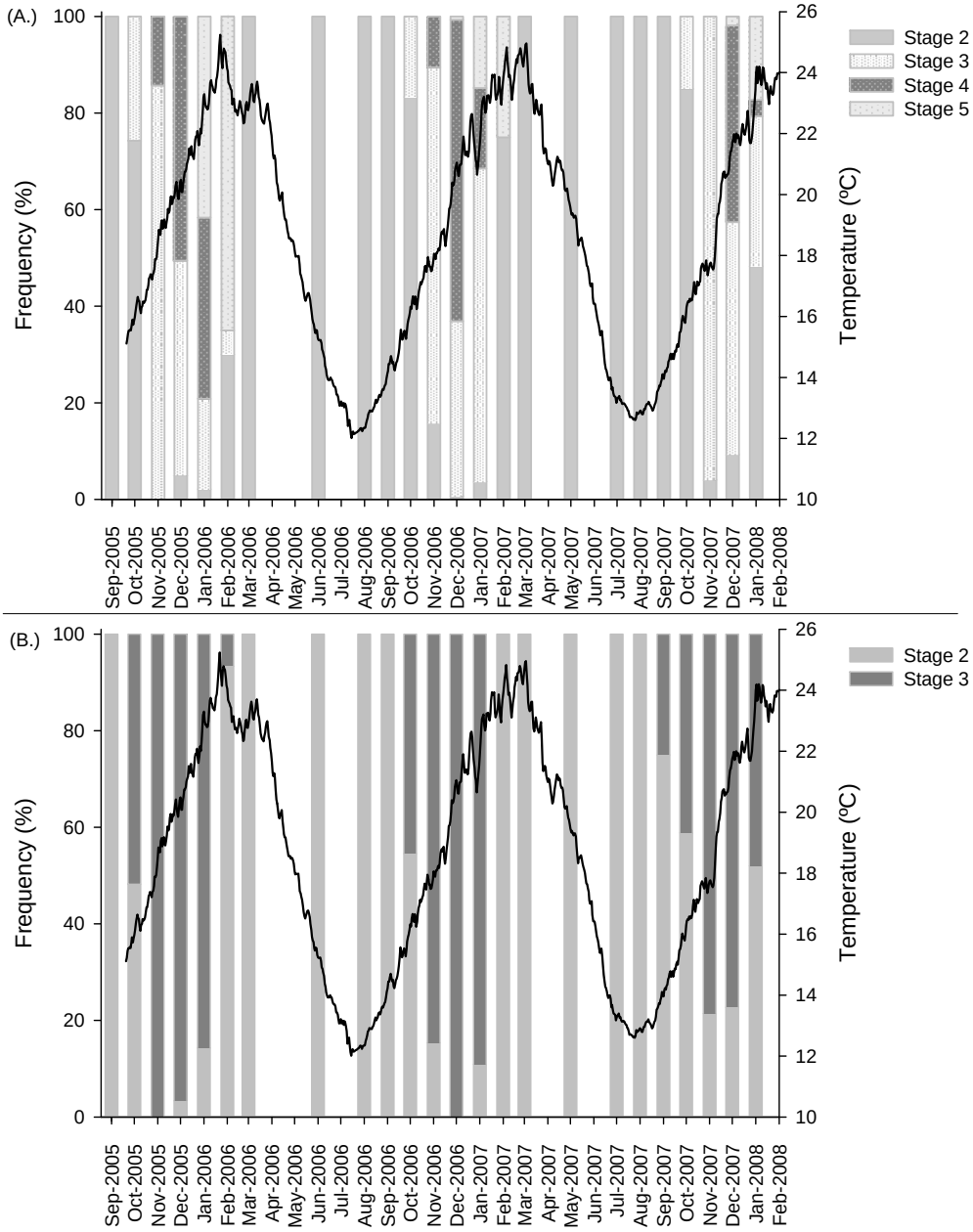


Figure 4.7. (A) Percent frequency of female macroscopic stages by month with temperature data overlaid. (B) Percent frequency of male macroscopic stages by month with temperature data overlaid. For both graphs the black line is daily average temperature at Western Shoal.

Spawning fraction and spawning frequency. The first mature spawning females were collected in November 2005. The estimate of spawning fraction for this sample was only 0.14. This was considerably lower than for the subsequent samples that were collected in December 2005, when spawning fraction ranged from 0.33 to 0.9 (Table 4.4). Only two samples with spawning females were collected in January 2006 and these had spawning fractions of 0.86 and 0.85. No samples of sufficient number were collected to estimate spawning fraction in February 2006, however, histological analysis of the ovaries collected at that time showed no evidence of spawning activity.

Spawning fractions were used to estimate spawning frequency (Table 4.4). These data suggested that in late November fish were spawning, on average, once every 7 days, but, by early December fish were spawning daily. This high rate of spawning was maintained until early January.

A similar pattern was evident for the 2006/07 season. The first spawning fish were identified in late November, when the spawning fraction was lower than for the December samples. In January, more samples were collected than during the previous season and spawning fraction estimates were considerably more variable, ranging from 0.14 to 1.0 (Table 4.5). No samples with spawning females were collected in February or later. The data indicated that in both seasons, spawning had begun by at least late November, occurred more frequently in December and continued through January but had ceased by early February.

In 2007/08, ovaries collected during November showed advanced development but no hydrated oocytes or post-ovulatory follicles were observed. The first sample with evidence of spawning was collected on 4th December, when spawning fractions ranged from zero to 0.73 (Table 4.6). The last sample with spawning fish was collected on the 11th of January. Spawning fraction during January was considerably lower than for December. The estimates of spawning fraction for this season were lower than for the previous two seasons.

Table 4.4. Estimates of spawning fraction for all samples collected in 2005/06 that showed evidence of spawning activity. Samples were collected outside this period and none contained spawning females. Spawning fraction and spawning frequency estimates are not presented for samples when n<3.

Sample date	Number of mature females	Number of spawning females	Spawning fraction	Spawning frequency
24 Nov 2005	7	1	0.14	7.00
1 Dec 2005	18	16	0.89	1.13
2 Dec 2005	10	9	0.90	1.11
3 Dec 2005	9	5	0.56	1.80
4 Dec 2005	5	3	0.60	1.67
7 Dec 2005	3	2	-	-
8 Dec 2005	3	1	-	-
9 Dec 2005	6	2	0.33	3.00
11 Dec 2005	6	4	0.67	1.50
13 Dec 2005	6	5	0.83	1.20
14 Dec 2005	54	47	0.87	1.15
16 Dec 2005	31	20	0.65	1.55
18 Dec 2005	4	2	-	-
19 Dec 2005	2	1	-	-
21 Dec 2005	9	8	0.89	1.13
22 Dec 2005	4	0	-	-
28 Dec 2005	7	5	0.71	1.40
30 Dec 2005	5	3	0.60	1.67
4 Jan 2006	7	6	0.86	1.17
6 Jan 2006	13	11	0.85	1.18
All samples	209	151	0.72	1.38

To determine the period of greatest spawning activity, spawning fraction and spawning frequency estimates were calculated on a fortnightly basis from November 15th to January 31st for each season. The peak in spawning activity occurred in the first fortnight in December 2005 and 2007 but in the second fortnight of December 2006 (Fig. 4.8). Spawning fish were identified in four fortnights during 2005/06, five fortnights in 2006/07 but in only three fortnights during 2007/08 (Fig. 4.8).

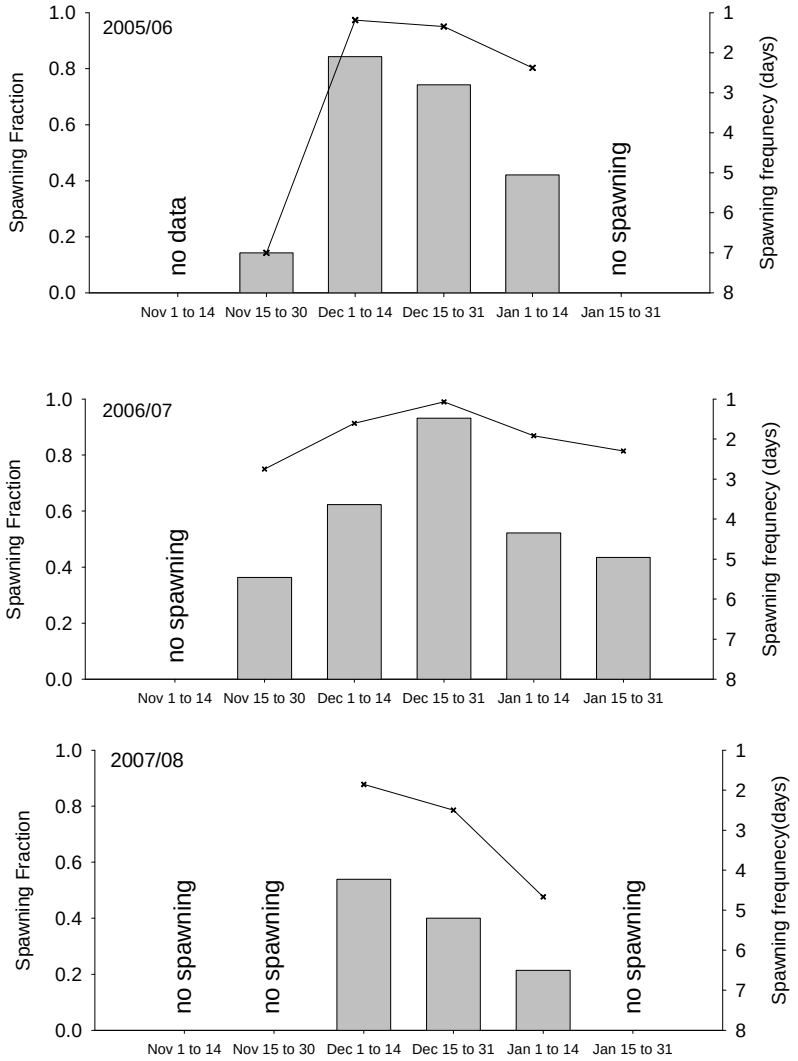


Figure 4.8. Fortnightly estimates of spawning frequency (line) and spawning fraction (bars) for each season from November 1st to January 31st. (Note: samples were collected in October and in February of each season, but these samples contained no spawning females).

Inter-annual variation in spawning activity was assessed by considering the peak two fortnights for each season which were from December 1st to 31st each year. Over the three years of the study, 385 mature females were examined from the month of December. The proportion of spawning to non-spawning females differed between years (χ^2=26.2, df = 2, $p<0.001$) due to the lower number of spawning females present during December 2007. This is reflected in the lower spawning fraction and higher spawning frequency for that year (Fig. 4.8).

Table 4.5. Spawning fraction estimates for all samples collected from the first to the last sample that contained spawning females for 2006/07. Samples were collected outside this period and none contained spawning females. Spawning fraction and spawning frequency estimates are not presented for samples when n<3.

Sample date	Number of mature females	Number of spawning females	Spawning fraction	Spawning frequency
28 Nov 2006	11	4	0.36	2.75
1 Dec 2006	14	10	0.71	1.40
5 Dec 2006	17	10	0.59	1.70
6 Dec 2006	4	3	-	-
8 Dec 2006	10	6	0.60	1.67
12 Dec 2006	4	4	-	-
13 Dec 2006	19	11	0.58	1.73
14 Dec 2006	7	7	1.00	1.00
17 Dec 2006	18	15	0.83	1.20
18 Dec 2006	6	3	0.50	2.00
21 Dec 2006	10	10	1.00	1.00
27 Dec 2006	11	11	1.00	1.00
28 Dec 2006	8	7	0.88	1.14
29 Dec 2006	21	14	0.67	1.50
3 Jan 2007	3	1	-	-
5 Jan 2007	9	7	0.78	1.29
10 Jan 2007	7	1	0.14	7.00
12 Jan 2007	9	7	0.78	1.29
17 Jan 2007	8	8	1.00	1.00
19 Jan 2007	9	2	0.22	4.50
23 Jan 2007	9	7	0.78	1.29
All samples	214	148	0.69	1.45

Table 4.6. Spawning fraction estimates for all samples collected from the first to the last sample collected with evidence of spawning for 2007/08. Samples were collected outside this period and none contained spawning females. Spawning fraction and spawning frequency estimates are not presented for samples when n<3.

Sample date	Number of mature females	Number of spawning females	Spawning fraction	Spawning frequency
4 Dec 2007	18	3	0.17	6
7 Dec 2007	10	5	0.50	2
12 Dec 2007	11	8	0.73	1.38
21 Dec 2007	6	0	-	-
28 Dec 2007	7	4	0.57	1.75
31 Dec 2007	2	1	-	-
9 Jan 2008	8	1	0.13	8
11 Jan 2008	6	2	0.33	3
All samples	68	24	0.35	2.83

The effect of fish size on spawning activity could only be tested for December 2005 because very few fish in the smallest size class were collected in the other two seasons. No effect of fish size was detected (χ^2=1.77, df = 2, p=0.413), as reflected in the similar estimates of spawning fraction and spawning frequency for the different size classes (Table 4.7).

4.3.5 Fecundity

Batch fecundity (B_f) was estimated from the number of hydrated oocytes in the Stage 4 ovaries. The relationships between B_f and CFL were linear and compared between years by analysis of covariance. The regression lines differed between years with that for 2007/08 having a much greater slope (Table 4.8). Similar results were obtained for the relationships between B_f and W_{gf}. The regressions were very similar in the first two seasons but in the third season, batch estimates were considerably higher for the same size fish than in the previous years (Fig. 4.9).

Table 4.7. Estimates of spawning fraction by length class for each season. Dash indicates no samples collected.

Season	Size class (CFL mm)	Number of mature females	Number of spawning females	Spawning fraction	Spawning frequency
2005/06	301-500	19	15	0.79	1.27
	501-700	65	52	0.84	1.19
	701 +	31	28	0.90	1.11
2006/07	301-500	-	-	-	-
	501-700	68	51	0.75	1.33
	701 +	37	28	0.76	1.32
2007/08	301-500	-	-	-	-
	501-700	32	16	0.5	2.00
	701 +	22	11	0.5	2.00

Table 4.8. Results from regression analyses between batch fecundity (BF) and fish size (CFL) and ovary-free weight (W_f) for samples of snapper from northern Spencer Gulf for the 2005/06, 2006/07 and 2007/08 seasons and results of ANCOVA between the regression lines for the three seasons. (*, significant at P = 0.01, n.a. indicates that this test was not necessary because the test for slopes was significant).

Season	Equation	n	r^2	*P*	Factor	df	F-ratio	*P*
2005/06	BF=1703.5 (CFL) - 814604	64	0.52	<0.000*	Slope	2,140	15.947	<0.000*
2006/07	BF = 2060.9 (CFL) -1000000	62	0.30	<0.000*	Intercept	n.a.		
2007/08	BF = 5638.6 (CFL) - 2955556	20	0.65	<0.000*				
2005/06	BF = 86.872 (W_f) - 121448	64	0.62	<0.000*	Slope	2,140	13.299	<0.000*
2006/07	BF = 103.17 (W_f) - 154499	62	0.32	<0.000*	intercept	n.a.		
2007/08	BF = 242.472 (W_f) - 385903.4	20	0.63	<0.000*				

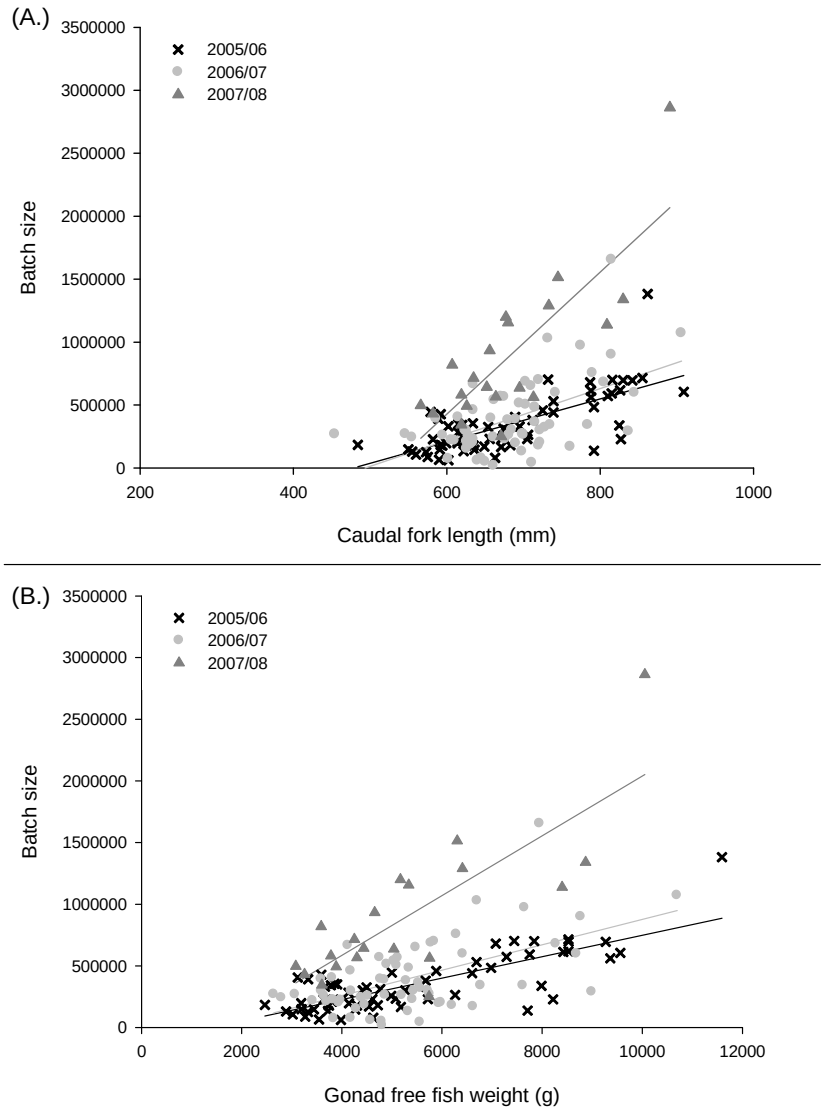


Figure 4.9. (A) Plot of batch size vs CFL with regression line fitted for each season and (B) plot of batch size vs W_{gf} with regression line fitted for each season.

4.4 Discussion

Snapper ovaries exhibited features associated with indeterminate fecundity. These were the co-occurrence of oocytes at different developmental stages and a continuous size distribution between maturity classes of oocytes, except for a gap between hydrated and advanced yolked oocytes (Hunter and Macewicz 1985). Furthermore, the simultaneous presence of oocytes at different developmental stages indicated that oocyte development was asynchronous. Studies in Japan (Matsuyama *et al.* 1987,1988) and New Zealand (Scott and Pankhurst 1992) have also concluded that the snapper is a multiple batch spawner with asynchronous oocyte development and indeterminate fecundity. No prior studies in Australia have documented reproductive mode of snapper.

GSI indicated that most reproductive development and activity occurred from November to January inclusive. The increase in GSI for both sexes was related to the presence of later stage (more mature) gonads. During October, the first Stage 3 ovaries caused a slight rise in the GSI. The peak in GSI in December was due to the high incidence of Stage 4 ovaries, whilst the decrease in January was due to the higher incidence of Stage 5 ovaries and the fewer Stage 4 ovaries. From March to September each year, all ovaries were at Stage 2, which coincided with the lowest GSIs. For males, high GSI was associated with a high proportion of Stage 3 males. The period when GSI was lowest, i.e. from March to September each year, occurred when all testes from mature fish were at Stage 2. This gave a broad indication of when spawning was likely to occur and corresponded with the timing of gonad development observed in New Zealand (Crossland 1977a) and the southern and south-eastern coastline of Australia (Ferrell and Sumpton 1998; Coutin *et al.* 2003), but spawning occurs earlier in more northern locations such as Moreton Bay on the east coast (Ferrell and Sumpton 1998) and Shark Bay on the west coast of Australia (Jackson and Cheng 2001).

GSI and macroscopic staging do not provide accurate estimates of spawning times or frequency. This information was obtained by microscopic analysis of gonads and demonstrated that the spawning season in northern Spencer Gulf began in November or early December each year. The duration of the spawning season in 2005/06 was a minimum of 43 days and a maximum of 77 days. During the 2006/07 season, spawning occurred over a period lasting at least 56 days and a maximum of 80 days and in the 2007/08 season spawning occurred over a period lasting at least 38 days and a maximum of 54 days. Previous estimates of the duration of the spawning season of snapper in South Australia and New Zealand have been from 3 ½ to 5 months, i.e. up to 150 days (Scott and Pankhurst 1992; Fowler *et al.*

2005a). The spawning seasons observed in northern Spencer Gulf during this study were considerably shorter.

Evidence of daily spawning in snapper was apparent from the co-occurrence in some ovaries of post-ovulatory follicles at different stages of degeneration and hydrated oocytes. Further evidence of daily spawning is apparent in the frequency with which samples containing spawning females were obtained. A total of 19 of 20 samples collected between 24th November 2005 and 6th January 2006, all 21 samples collected between 28th November 2006 and 23rd January 2007 and 7 of 8 samples collected between 4th December 2007 and the 11th January 2008 included spawning females. Thus, at least for the December period and probably somewhat longer, spawning fish were present on almost every sampling occasion. The snapper of New Zealand are also considered to spawn over consecutive days (Scott *et al.* 1993) but daily information on spawning is not available from elsewhere.

Spawning began when water temperature was between 18ºC and 20ºC and continued at times when water temperatures reached daily extremes over 25ºC. This result differs considerably from that found for New Zealand snapper where spawning began when sea surface temperature was between 15ºC and 16ºC and finished at temperatures between 19ºC and 21ºC (Scott and Pankhurst 1992). Although the comparison is between sea surface temperature in New Zealand and sub-surface temperature in South Australia, the different results are considerable and seem unlikely to be explained by the different techniques used to measure temperature, especially as the surface temperatures in New Zealand were lower. The temperature range over which spawning occurs in Japan, 15ºC to 21ºC (Kojima 1981; Foscarini 1988), is closer to that observed in New Zealand than in South Australia's northern Spencer Gulf.

The timing of spawning by snapper varies considerably throughout the Australian range of the species. In the northern part of the range, i.e. Moreton Bay, Qld and Shark Bay, WA, snapper spawn during the austral winter months (Ferrell and Sumpton 1998; Jackson and Cheng 2001) when day length is short and water temperatures are dropping. In the south, spawning occurs when day length is relatively long and water temperatures are increasing. Consequently, it seems unlikely that photoperiod is an important cue for spawning by snapper. In northern Spencer Gulf, the timing of spawning appears to correspond with water temperatures of at least 19.5ºC. Temperatures increase from winter lows before GSI increases and the GSI drops earlier than temperature indicating that the spawning season is entirely encompassed by the spring-summer periods of warm water (>19ºC).

The relationships between the number of eggs spawned in a batch and fish size (both length and weight) were indistinguishable between the first two seasons. In the third season, however, batch sizes were considerably higher. This was reflected in the considerable differences in the slopes of the regression lines. Inter-annual differences in batch sizes have not been reported before for snapper, although such differences commonly occur in other species (e.g. Hunter *et al.* 1985; DeMartini 1991) and are sometimes considered to be density-dependent and compensatory (Bagenal 1973; Trippel 1995).

This study has identified intra-annual variations in the timing and length of the spawning season as well as the frequency of spawning events. Furthermore, inter-annual variations in these parameters as well as batch fecundity were also observed and have considerable implications for egg production and consequently the number of potential recruits available to the population. The variation in these reproductive parameters adds weight to the argument that to test hypotheses about the effect of egg production on recruitment, inter- and intra-annual changes in spawning activity, output and perhaps other parameters (such as egg quality) need to be taken into account (Marshall and Frank 1999).

Spawning timing indicates that recruits in northern Spencer Gulf are likely to originate from early December until the first two weeks of January. The differences between years in the length and temporal distribution of spawning events indicate that the numbers of spawning events would differ between years. Given that the average annual spawning frequencies and the maximum and minimum spawning periods observed, an average fish in 2005/06 would have spawned at least 31 times and as many as 55 times, in 2006/07 from 38 to 55 times and in 2007/08 from 13 to 19 times. Thus, if recruitment is related directly to the numbers of spawning events, the 2008 year-class would be expected to be weaker than those of 2006 or 2007.

The change in batch fecundity during the 2007/08 spawning season complicates predictions of recruitment strength. The slope of the regression between batch size and fish weight, which provides a measure of the number of eggs per kilogram of gonad free fish weight, differed between years. The last season studied had a considerably higher number of eggs produced per kilogram of gonad-free fish weight. Thus, although spawning was less frequent than during the first two years, the number of eggs produced at each spawning event was much higher. If recruitment was related directly to the number of eggs spawned in a batch, the 2008 year-class would be expected to be stronger than in either 2006 or 2007. Trawl sampling has indicated that recruitment of 0+ snapper in northern Spencer Gulf was strongest in 2006, weaker in 2007 and very poor in 2008 (Chapter III). These changes in recruitment strength in

2006 and 2007 occurred independent of changes in the reproductive biology. However, the spawning pattern changed in 2007/08 and very few recruits were spawned successfully (Chapter III).

If differences in batch and spawning frequencies are major determinants of recruitment success, the temporal origin and relative numbers of recruits for the 2006 and 2007 year-classes are predicted to be similar, with most recruits being spawned during December and early January. The 2007/08 spawning season is likely to differ with recruits expected to originate from a shorter period but at a higher rate per spawning event. A practical test of these hypotheses is to identify the successful spawning periods of each reproductive season. This can be done by back-calculating the spawn dates of successful recruits from the microstructure of their otoliths. This was the approach of the analytical work undertaken in Chapter V.

Chapter V

The early life history of snapper, *Chrysophrys auratus*, and the impact of a variable environment on recruitment

5.1 Introduction

Year-class strength in fish populations is thought to be set very early in the life history such that abundance of 0+ recruits often reflects future year-class strength (Houde 1987). Variation in the recruitment of 0+ fish is therefore important to fish population dynamics (Sale 1990; Doherty and Fowler 1994) and can result from changes in egg production and the mortality of eggs and larvae (Sissenwine 1984; Rothschild 1986). The timing of spawning in fish is in turn affected by various physical parameters including lunar phase or tidal variation (Robertson *et al.* 1999) and temperature (Bye 1984; Sheaves 2006). Mortality of eggs and larvae is also affected by the physical environment (Houde 1987; Bradford and Cabana 1995; Myers 1998). Thus, the complex relationship between the environment and the early life stages results in variable recruitment (Fogarty *et al.* 2001). In many multiple batch spawning species, eggs and larvae are exposed to a variety of environmental conditions which vary in suitability for growth and survival (Winemiller and Rose 1993). Sometimes, only part of a spawning season results in recruitment (Methot 1983; Cargnelli and Gross 1996; Wright and Bailey 1996) and in longer-term studies the timing of successful spawning has often been demonstrated to be inter-annually variable (Fowler and Jennings 2003; Wright and Gibb 2005).

Determining precisely when year-class strength is set and the physical environmental conditions that are suitable for successful recruitment is difficult. Otolith microstructure has been a source of valuable information on the temporal dynamics of successful spawning and settlement rate in fish (Sogard *et al.* 2001; Fox *et al.* 2007). The data obtained from such otolith analyses, coupled with detailed environmental data and information on the spawning activity of adults, can be used to examine intra-annual effects of environmental variation and spawning on the early life stages of fish (Anderson 1995; Campana 1996; Kurita *et al.* 2004; Bauman *et al.* 2006). Furthermore, this information may provide some explanation for inter-annual variation in the abundance of juveniles and ultimate year-class strength (Campana

1996). There are, however, many different environmental factors that can impact on spawning activity and mortality of eggs and larvae. Spawning and settlement patterns in some species are correlated with the lunar cycle and hence tidal variation (Robertson *et al.* 1999; Gladstone 2007), and are likely to impact on the timing of recruitment. Physical environmental parameters such as temperature and dissolved oxygen can also kill eggs and larvae or compromise growth rate which in turn may result in higher mortality due to increased predation (Houde 1987).

The population dynamics of snapper, *Chrysophrys auratus*, in northern Spencer Gulf (Fig. 1) is dominated by large inter-annual variation in recruitment of 0+ fish to the inshore nursery grounds, in particular around Western Shoal (Fowler and Jennings 2003; Chapter III). There is some indication that this variation in recruitment drives the State-wide variation in year-classes available to fishers (Fowler and Jennings 2003; Fowler *et al.* 2005a) but the conditions that are required to spawn a strong year-class are not known. In New Zealand, water temperature has been implicated in strong juvenile recruitment (Francis 1993; Francis *et al.* 1997) and in South Australia it was thought to contribute to variation in 0+ recruitment (Fowler and Jennings 2003). The spawning and nursery areas in South Australia's northern Spencer Gulf experience the greatest environmental extremes in the state's marine coastal waters which may impact on spawning success and 0+ recruitment.

In northern Spencer Gulf, water temperatures vary by as much as 14ºC between winter and summer (Nunes and Lennon 1986; Chapter III), whilst it also has the greatest tidal variation of any part of South Australia, i.e. up to 4.32 m at Port Augusta (Noye 1984). Tidal currents can be extreme and at the narrow neck at the top of the gulf between Pt Lowly and Ward Spit (Fig. 1), a tidal race develops with currents likely to exceed 1 $m.s^{-1}$ (Noye 1984). South Australia is also one of the few parts of the world where periodically almost no tidal movement occurs for periods of up to 24 hours, known locally as "dodge" tides (Noye 1984). Accurate tide predictions are freely available for Whyalla, a major port in the centre of the study region. The daily fluctuation in tidal movement at Whyalla is large by temperate standards, varying by up to 3.1 metres (Flinders Ports 2008). Such dramatic environmental variation may influence the recruitment process because the timing of spawning and settlement in fish are often linked to tidal variation and/or phase-of-the-moon (Robertson *et al.* 1999; Gladstone 2007).

The general aim of this chapter was to determine some of the environmental conditions required to spawn successful recruits of 0+ snapper in northern Spencer Gulf. To do this, some early life history traits of successful 0+ recruits are compared across three consecutive

years which experienced large differences in 0+ recruitment (Chapter III). The specific objectives were: one, to determine the specific spawn and settlement dates of snapper from analysis of the microstructure of otoliths, two, to calculate the larval duration and three, to compare the timing and variation of these early life history traits with temperature, lunar and tidal parameters. The spawn dates of the recruits are also compared against spawning activity, measured from adults (Chapter IV), to provide an indication of its effect on recruitment processes.

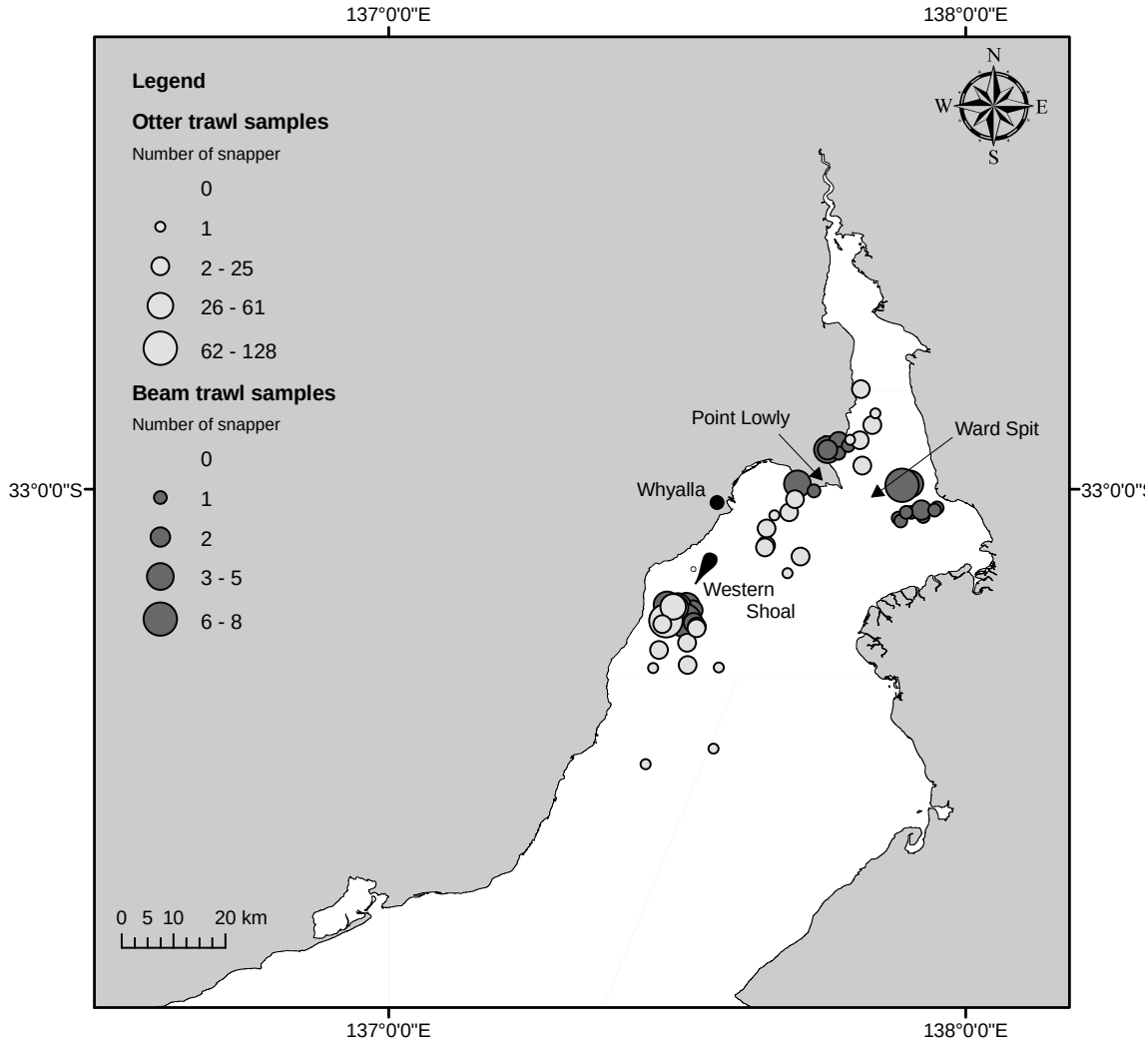


Figure 5.1. Map of the study region, northern Spencer Gulf showing the location of all trawls that captured 0+ snapper between 2006 and 2008.

5.2 Methods

5.2.1 Water Temperature

Water temperature was recorded hourly at Western Shoal by a temperature data logger (StowAway TidBit™). This was attached to a navigational beacon in September 2005. The data were retrieved three times during the study, the last occasion being April 2008.

5.2.2 Field sampling techniques

Young-of-the-year snapper (0+ age class) were collected from northern Spencer Gulf by otter and beam trawl sampling undertaken from 2006 to 2008, described in Chapter III (Figure 5.1). The timing of the sampling was based on knowledge of the spawning period for snapper in northern Spencer Gulf (Fowler *et al.* 2005a) and the egg and larval development periods of the species (Pankhurst *et al.* 1991). Catches in the trawls varied dramatically between years reflecting 0+ recruitment. Thus a different number of fish was available for analysis each year. The otter trawling caught 253, 67 and three 0+ snapper each year respectively (Chapter III). Fish collected in the beam trawl (Chapter III) provided additional samples for otolith analysis to those from the otter trawl, making available a further 55 0+ snapper in 2006 and 30 in 2007.

5.2.3 Laboratory processing techniques

All 0+ snapper collected in the trawls were measured for caudal fork length (CFL) from the tip of the snout to the posterior end of the middle caudal rays to the nearest mm and weighed to the nearest 0.01 g. The sagittal otoliths were removed, cleaned of extraneous tissue and dried by rubbing on silk cloth. They were stored dry in plastic snap-lock bags until the time of processing.

5.2.4 Otolith preparation

Transverse sections of the sagittae have been shown to be the best preparation to expose the microstructure of the otoliths of juvenile snapper (Fowler and Jennings 2003). These sections were prepared by grinding and polishing. One sagitta from each fish was mounted on a microscope slide using CrystalBond™ and ground from the anterior end towards the core using a Gemmasta grinding wheel with a 45 μm diamond sanding disc and then polished on 9 and 6 μm imperial lapping film. The polished surface was then mounted at the centre of a microscope slide and the grinding and polishing was done from the posterior end to produce a section of ~50 μm thickness. In some cases, a final polish was done using 0.05 μm alumina powder on a suede cloth.

5.2.5 Otolith analysis

Each sectioned otolith was examined using an Olympus compound microscope at magnifications of 400x to 1000x, with the image displayed on a computer screen via a video camera and Optimas image analysis software. Immersion oil was used to enhance the image by clearing the surface scratches. A count of the post-settlement increments was made from the settlement mark to the proximal surface between the sulcus and the ventral apex along the dark band identified as the sagittal-subcupular meshwork fibre zone (SMF; Francis 1994b), which was the axis that provided the clearest sequence of micro-increments at 400x. The pre-settlement increments were counted from the primordium in the opposite direction to the SMF line to the settlement mark at 1000x magnification (Fowler and Jennings 2003).

Increments were counted blind with respect to fish length, and each otolith was examined on three separate occasions. If the counts differed by more than 5%, the otolith was rejected, otherwise the mean was accepted as the best estimate of the count, retaining the separate counts of pre- and post-settlement increments. The age of the fish was calculated by summing the pre- and post-settlement increments, but with the addition of four days to accommodate the two days of egg development and that no increments formed for two days after hatch (Pankhurst *et al.* 1991).

The date of settlement of each wild-caught juvenile was calculated by subtracting the number of post-settlement increments from the date of collection. The date on which it was spawned was calculated by subtracting the total estimated fish age from the date on which it was captured. Estimates of the success and timing of spawning and settlement were gained by calculating a frequency distribution of the spawn and settlement dates for each year.

The average water temperature that each 0+ snapper experienced during the larval life was determined from the temperature logged at Western Shoal. The relationship between pre-settlement duration and average temperature that all fish were exposed to during their pre-settlement period was then described with regression analysis. This relied on the assumption that the temperature logged at Western Shoal was representative of that experienced by the fish during their pre-settlement life.

5.2.6 Analyses

The estimation of spawn and settlement dates provided frequency distributions of the numbers of successful recruits that were spawned and settled on particular days. These data were assessed for any temporal periodicity using autocorrelation analysis. These analyses were done for data from 2006 and 2007, but not 2008 because only three 0+ snapper were collected

from the trawl survey in that year. The frequency distributions of spawn dates, from the date of the first successfully spawned fish to the last, were made stationary by first order differencing (Chatfield 1996). The same process was done for the frequency distribution of settlement dates for the period of the first to last settlement dates.

To test whether the successful 0+ recruits were spawned uniformly throughout the lunar cycle the days when recruits were spawned were converted to a day in the 29-day lunar cycle, where the new moon occurred on day 1 and the full moon on day 15. The total number of recruits that were spawned on each day of the lunar cycle was then calculated for each season. Rayleigh's test was used to determine if the distribution was stable throughout a lunar cycle (Zar 1999). The same process was done for the settlement date frequency distributions. Support for a relationship between the spawn or settlement date frequencies and a lunar cycle could also be derived from the autocorrelation analyses if a significant autocorrelation at lag 15 and/or 29 was obtained, dependent on whether a response was semi-lunar or lunar.

The effect of temperature fluctuations on successful spawning was considered by cross-correlation analysis between the frequency distribution of spawn dates and the maximum daily difference in hourly logged temperature at Western Shoal. A significant correlation at lag 0 would provide evidence for this hypothesis. That there may be an absolute effect of temperature on spawning success was tested by cross-correlation of frequency distributions of spawn dates and the average daily temperature at Western Shoal (1st order differenced to account for the upward trend). Cross-correlation analysis was also used to consider the relationship between daily tidal range and frequency distributions of spawn dates and settlement dates. All cross-correlation analyses were done for lag 0 without lagging the data because the tests were to assess the effect of the environment at or immediately after spawning or settlement. The water temperature data used in these analyses were logged at Western Shoal and the tidal data were the predictions for Whyalla, provided by the National Tidal Facility.

The daily average number of recruits for each of a series of water temperature ranges was calculated to determine the range of, and most suitable temperatures in which, the 0+ snapper collected were spawned. Days were categorised into 1ºC temperature brackets according to the average temperature recorded at Western Shoal. Then the daily average and standard error of the number of 0+ snapper that were spawned was calculated for each temperature bracket. This procedure was done for a period that encompassed all spawn dates and the whole spawning season in northern Spencer Gulf (Chapter IV), i.e. from November 15th to February 28th inclusive. The period included days with temperatures from 18 to 25ºC each

year. This was done for fish collected in 2006 and 2007 but not 2008 as only three fish were available that year.

5.3 Results

5.3.1 Water temperature

The water temperature data logged at Western Shoal are described in detail in Chapter III. The average daily temperature data from October to May each season is presented in Figure 5.2 to aid comparison between years. Some major differences were evident between years. Water temperature in February 2007 was consistently higher than the other years and in November 2007 water temperature rose much more rapidly than in either of the previous years. In March 2008 a period of exceptionally warm weather resulted in a rapid rise in water temperature from 21.4ºC to reach the maximum for the season at 24.5ºC. Despite the data logger being at a depth of approximately six metres, daily temperature fluctuations were considerable, up to 2.7ºC, and throughout the summer months, regularly exceeded 1.5ºC (Fig. 5.3).

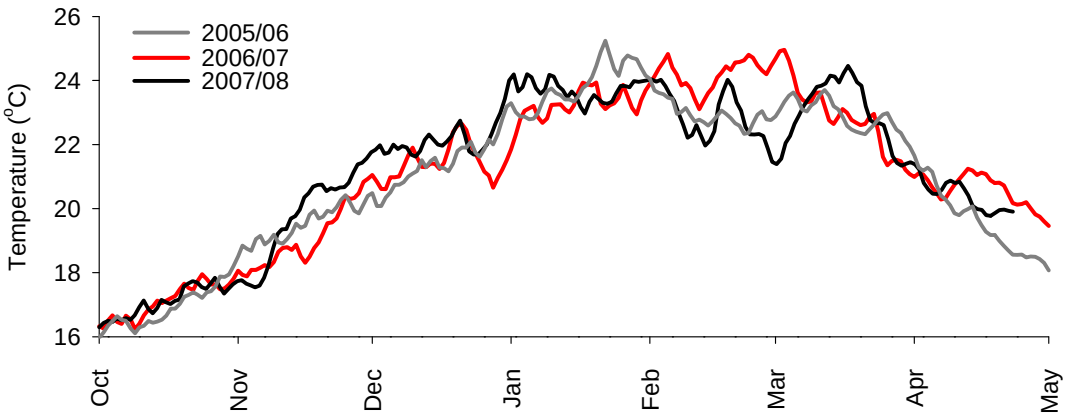


Figure 5.2. Daily average temperature calculated from hourly logged data at Western Shoal from 1st October to 1st May for the 3 seasons.

5.3.2 Spawn dates

2005/06

Successful recruits captured in the trawl surveys were spawned between late November and mid February but the distribution of spawn dates was not consistent throughout this period (Fig. 5.3). There were two distinct modes in the spawn date frequency distributions, i.e. around the 26th December and the 5th January. There were at least two other peaks of lower magnitude, i.e. mid-January and around the 1st February. No peaks corresponded with either full or new moon phases but were close to the quarters.

The earliest successful recruit found during the 2005/06 season was spawned on the 27th November when the average daily water temperature was 19.9ºC, and temperatures were rising. The last spawned fish was spawned on the 7th February when average daily water temperatures were 23.0ºC and falling (Fig. 5.3). Thus, there was a period of 83 days during which spawning ultimately led to successful recruitment. The longest consistent period during which spawning led to daily recruitment was from 10th December to 22nd January, a period of 33 days. During this period average daily water temperatures rose from 21.1ºC to 25.2ºC.

More 0+ recruits were spawned on days between 21ºC and 22ºC than days in any other temperature range (Fig. 5.4). No 0+ recruits were spawned on days below 19ºC. The water temperatures most suitable for 0+ snapper to be spawned successfully were between 20ºC and 25ºC, close to the maximum temperatures observed in the study. The cross-correlation analyses between spawn date and average daily water temperature and daily water temperature variation yielded non-significant results (Table 5.1).

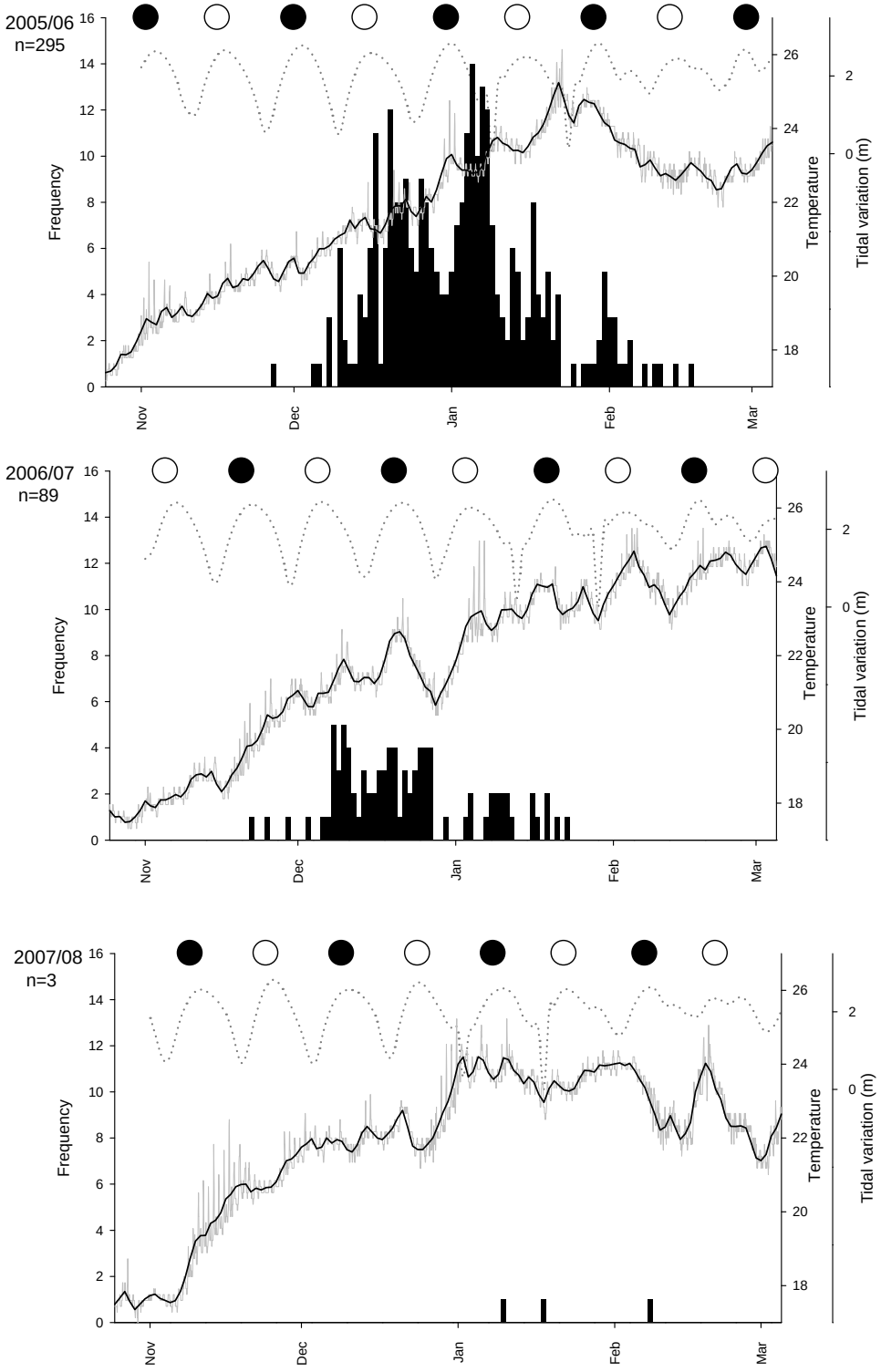


Figure 5.3. Spawn date frequency distributions for 0+ snapper collected in beam and otter trawl surveys from 2006 to 2008 (bars). The dotted grey line shows maximum daily tidal variation, and the solid dark line average daily temperature with hourly logged temperature in light grey behind. Dark circles indicate the new moon and open circles indicate the full moon.

Table 5.1. Cross-correlation analysis for lag 0 for several time series of environmental variables and spawn and settlement date frequencies. No significant cross-correlations were identified i.e., none exceeded the 95% confidence intervals.

Time Series	Year	Lag 0	
		CCF	95% C.I.
Spawn date frequency and average daily temperature	2005/06	0.053	±0.1826
	2006/07	0.158	±0.1826
Spawn date frequency and daily temperature variation	2005/06	0.104	±0.1826
	2006/07	-0.104	±0.1826
Spawn date frequency and maximum tidal variation	2005/06	0.014	±0.1754
	2006/07	0.097	±0.1734
Settlement date frequency and maximum tidal variation	2005/06	0.01	±0.1754
	2006/07	0.056	±0.1734

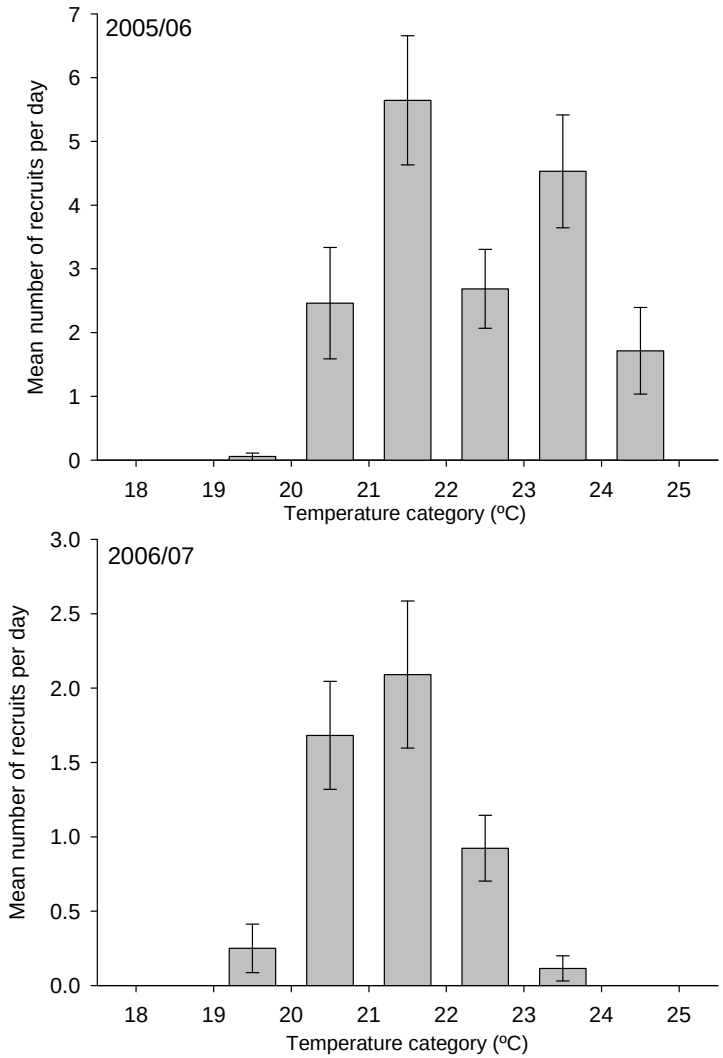


Figure 5.4. The mean number of recruits spawned each day in 1ºC temperature brackets for the 2005/06 and 2006/07 seasons.

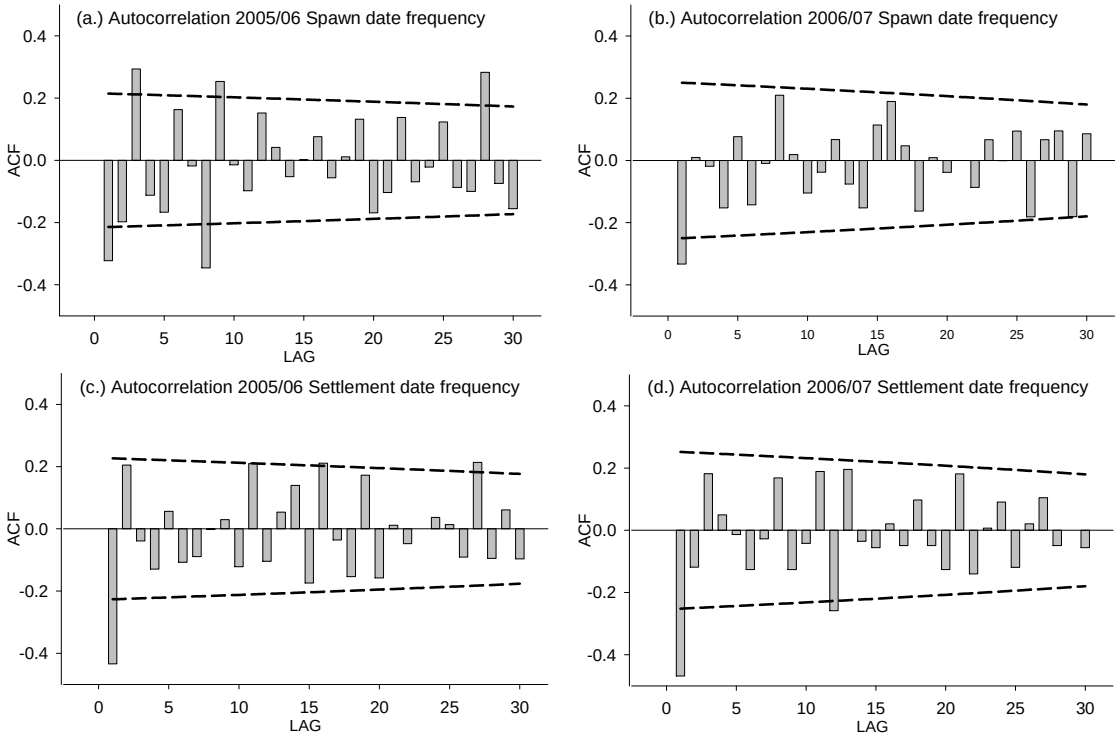


Figure 5.5. Autocorrelation graphs for spawn and settlement date frequencies for 2005/06 and 2006/07 from lag 1 to 30. Dashed lines are 95% confidence intervals. Significant lags are those that exceed these confidence intervals. ACF = autocorrelation function.

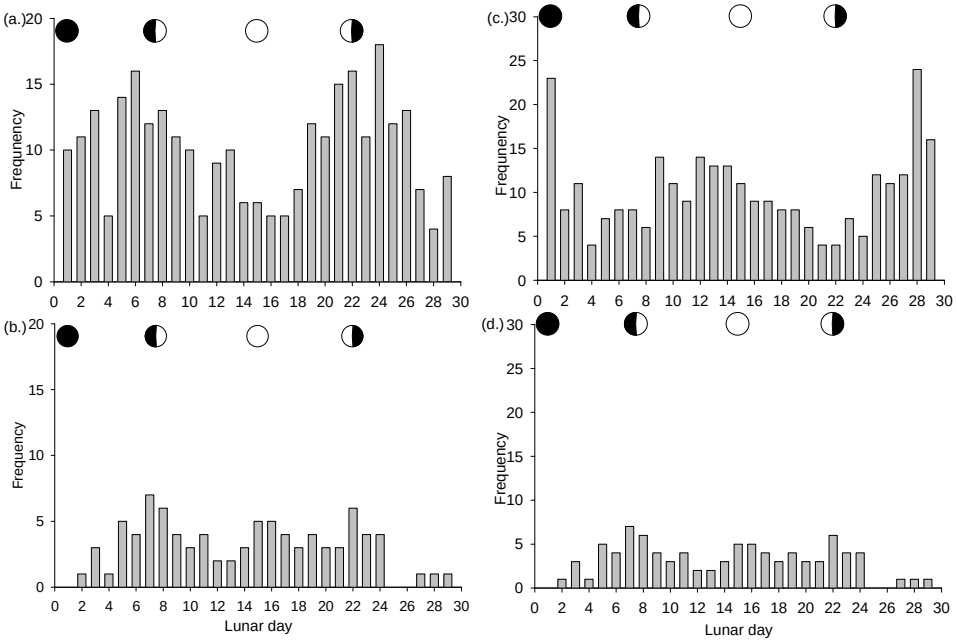


Figure 5.6 (a.). Number of 0+ recruits spawned on each lunar day that were captured in the trawl surveys of 2006; (b.) the same for 2007; (c.) Frequency of 0+ recruits that settled on each lunar day that were captured in the trawl surveys of 2006 and (d.) the same for 2007. Dark circles indicate the new moon and open circles indicate the full moon with lunar quarters also indicated.

There was some short-term autocorrelation in the frequency distribution of spawn dates, hence the significant negative autocorrelation at lag 1 day and positive autocorrelation at lag 3 days (Fig. 5.5a). This indicated that the day-to-day spawning success was related. Longer-term periodicity was also identified, with positive autocorrelations at lag 9 and 28 days. This indicates that the four modes were separated by 9 days although they were not particularly discrete. The lag 28 day autocorrelation was a result of the two broad periods of successful spawning. This was close to that anticipated for a lunar cycle. The periods of spawning success were, however, very broad and the modes did not correspond with either the full or the new moon, but rather, they fell on the lunar quarters (Fig. 5.3). The distribution of spawn dates of successful 0+ recruits was not uniform around the lunar cycle ($Z = 32.203$, $P < 0.001$). There were two modes in the distribution, around the first and last quarters (Fig. 5.6a), but some recruits were spawned on all days during the lunar cycle.

The tidal fluctuations were considerable over the period but did not correspond with the modes in the distribution of spawn dates (Fig. 5.3) and consequently no significant effect of tide was detected at lag 0 (Table 5.1). Some successful spawning occurred from days with very little or no tidal range as well as on days with the largest tidal range; however, none of the peaks in recruitment were associated with either very large or very small tidal ranges (Fig. 5.3).

2006/07

The frequency distribution of spawn dates was not stable throughout the period of the spawning season and differed from the previous season in that there were no discrete peaks. In contrast, there were two periods of consistent spawning success in December and January, but of reduced magnitude (Fig. 5.3). The period of spawn dates between the earliest spawned to last spawned recruit was 63 days, significantly shorter than for the previous year. The longest period during which spawning led to successful daily recruitment was also shorter at 20 days, i.e. from 6th to 26th December. Average daily water temperature was rising for the early part of this period from 21.0ºC to 22.5ºC on 20th December and then dropped rapidly until 26th December to 21.2ºC. The second period during which spawning led to successful recruitment lasted for 5 days in early January when temperatures had increased again and were relatively stable ranging from 22.7ºC to 23.2ºC.

The first and last successful recruits in 2006/07 were spawned earlier than in the previous year. The earliest recruit in 2006/07 was spawned on the 22nd November when the average water temperature was 19.6ºC and temperature was rising. The latest successful recruit fish was spawned on the 23rd January when the average water temperature was 23.2ºC (Fig. 5.3).

In contrast to the previous year, water temperature continued to rise after the last recruit was spawned. Recruitment resulted from spawning that occurred on days between 19 and 24ºC, but not from 25ºC days (Figure 5.4). Similar to the previous season, days in the 21 to 22ºC range had the highest mean number of recruits. Most 0+ recruits were spawned from a more restricted range of temperatures than the previous year, on days when water temperature was between 20 and 23ºC in 2006/07 (Figure 5.4). The cross correlation between daily average water temperature and daily water temperature variation again yielded non-significant results.

No periodicity was detected in the frequency distribution of spawn dates, i.e. no significant positive autocorrelations were detected (Fig. 5b). A significant negative autocorrelation was detected at lag 26 (Fig. 5b) but this result should be interpreted with caution because the length of the time series tested (66 days) is less than that recommended of 3 times the lag (Chatfield 1996), and the result was only marginally significant. The distribution of spawn dates of successful 0+ recruits sampled was not uniform around the lunar cycle ($Z = 26.257$, $P < 0.001$). There was one clear mode in the distribution, occurring around the first quarter (Fig. 5.6b). Some recruits were spawned throughout the lunar cycle but very few from around the new moon (Fig.5. 6b).

The tidal fluctuations were considerable over the period when successful recruits were spawned but no obvious correlation between the distribution of spawn dates and tidal range were observed. This was confirmed by the cross-correlation between tide range and the frequency distribution of spawn dates in which no significant correlations were obtained (Table 5.1). As in the previous season, some recruits were spawned on days with very little or no tidal range as well as on days with a large tidal range.

2007/08

There were no protracted periods from which spawning activity led to the successful recruitment as only three successful recruits were captured in the trawl survey. These fish were spawned later in the season than most recruits in either of the previous years. The spawn dates for these fish were the 10th and 18th January and the 8th February (Fig. 5.3) and they were spawned when the water temperatures were 24.2, 23.0 and 23.0ºC, respectively.

5.3.3 Settlement dates

2005/06

The frequency distribution of settlement dates in 2005/06 was similar in shape to the distribution of spawn dates, with two distinct modes early in the series separated by 14 days, and two other lower peaks occurring later in the season (Fig. 5.7). Settlement occurred over

an 83 day period from the 19th December to the 11th March, with settlement occurring every day from 30th December to 13th February. Some periodicity was detected in this distribution, with significant positive autocorrelations detected at lag 16 and 27 (Fig. 5.5c). Some settlement occurred on all different moon phases and on all tidal extremes, however, the two major modes, occurred on the 12th and 26th January, and were 3 days before the new and 2 days before the full moons, respectively. The distribution of settlement dates of successful 0+ recruits was not uniform around the lunar cycle ($Z = 23.224$, $P < 0.001$). There were two modes in the distribution around the new and full moons (Fig. 6c), but some recruits settled on all days during the lunar cycle. No cross-correlations between tidal height and settlement frequency were significant (Table 5.1).

2006/07

In 2006/07, there were fewer recruits spread out over the settlement season, so the frequency distribution of settlement was considerably lower compared to the previous season. The frequency distribution of settlement dates was similar to the distribution of spawn dates. Settlement occurred over 60 days from 16th December to 13th February, with a period of consistent settlement from 29th December to 21st January (Fig. 5.7). A significant negative autocorrelation was detected at lag 12 (Fig. 5.5d), however, given the low numbers settling, this could not be considered evidence for periodicity. There were no well defined modes to cross reference with lunar phase, however, the distribution of settlement dates of successful 0+ recruits was not uniform during the lunar cycle ($Z = 27.644$, $P < 0.001$). Very little settlement of successful recruits occurred around the new moon (Fig. 5.6d) but some settlement occurred at all other lunar phases. No significant effect of tidal variation was detected in the cross-correlation analysis (Table 5.1), and this was evident from Figure 5.7 where settlement was relatively stable in early January over a variety of tidal conditions.

2007/08

The three 0+ snapper captured in 2008 settled on the 31st January, 6th February and 3rd March (Fig. 5.7). This was later than most fish from either of the previous seasons.

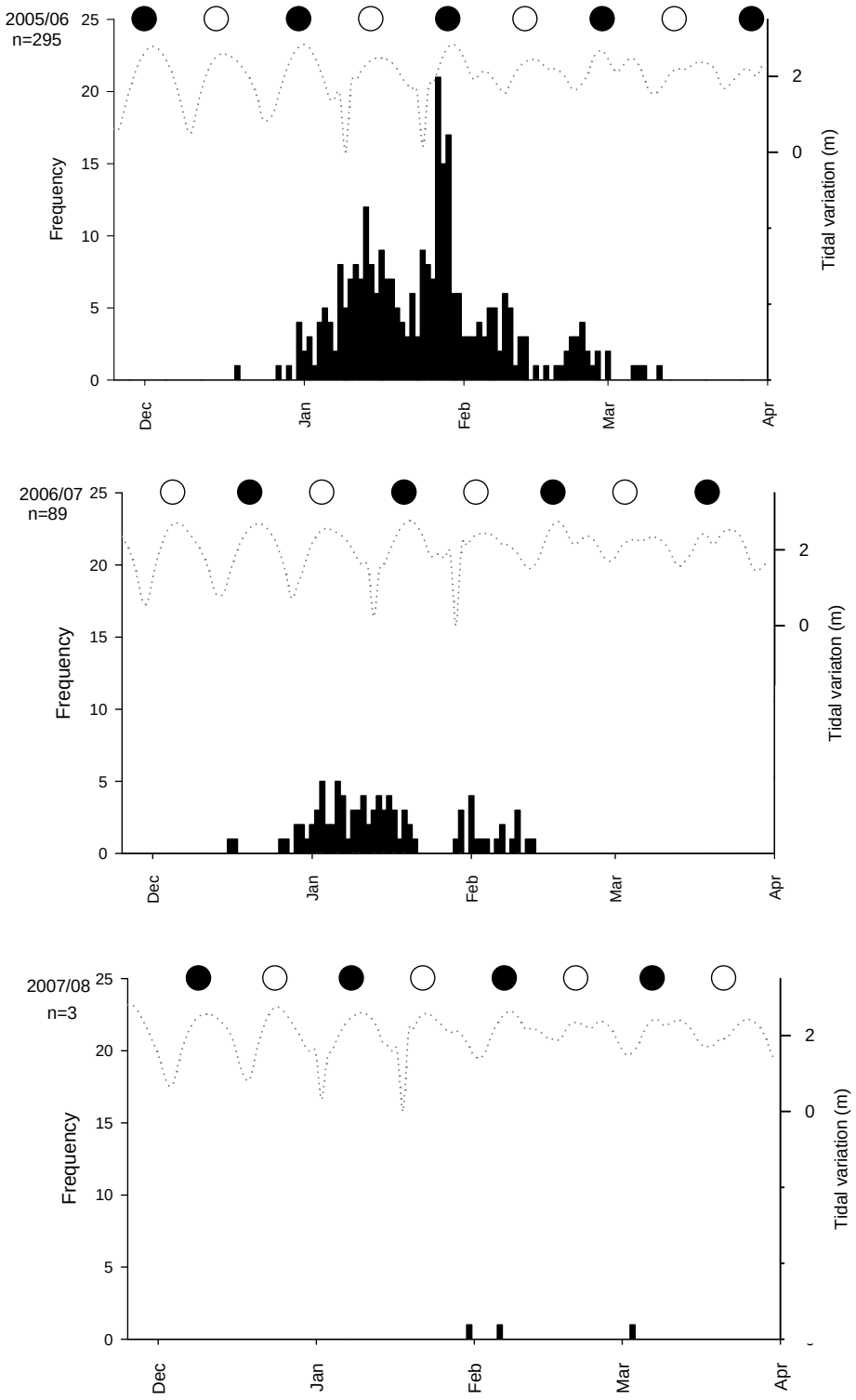


Figure 5.7. Bars show the frequency distributions of settlement dates for 0+ snapper collected in beam and otter trawl surveys from 2006 to 2008. The dotted line is maximum daily tidal variation. Dark circles indicate the new moon and open circles indicate the full moon.

5.3.4 Pre-settlement duration

The pre-settlement duration of fish collected in 2006 ranged from 17 to 27 days with a mean (± s.e.) of 22.0 days (± 0.1) (Fig. 5.8). In 2007, the pre-settlement durations ranged from 20 to 27 days with a mean (± s.e.) of 23.4 days (± 0.2). As such, the shorter durations from the previous year were not observed. In 2008, the 3 fish captured had pre-settlement durations of 19, 21 and 24 days (Fig. 5.8). Pre-settlement duration differed significantly between samples collected in 2006 and 2007 (Kolmogorov-Smirnov statistic= 2.46, $P < 0.001$) but comparisons with 2008 were not made due to the low sample size.

In 2006, the pre-settlement durations decreased with temperature but the relationship was very weak. Water temperature explained less than 1% of the variation in pre-settlement duration (Fig. 5.9). In 2007, the relationship was not significant (Fig. 5.9). The relationship was not calculated for 2008 because of the low numbers of fish collected.

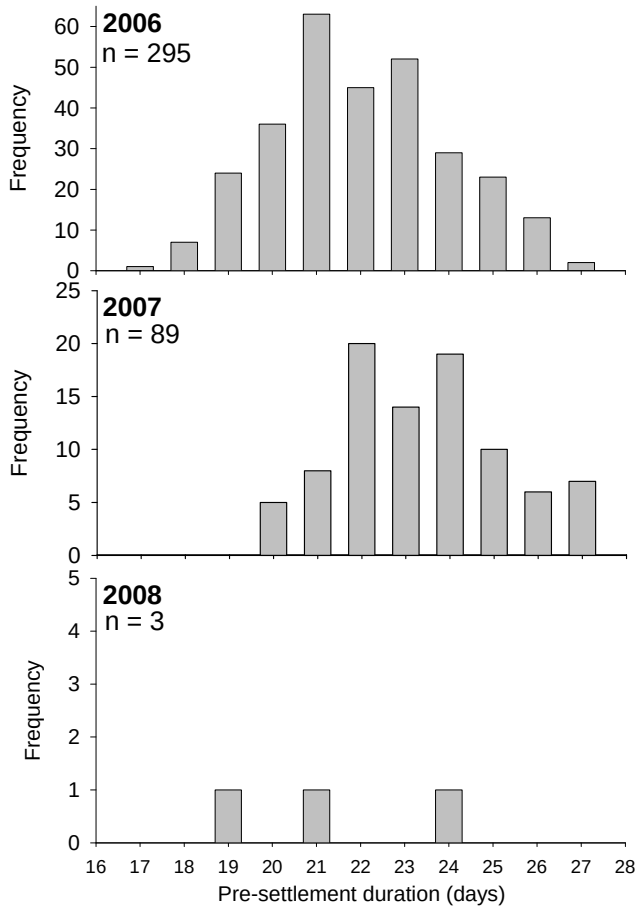


Figure 5.8. Frequency distributions of pre-settlement durations measured from the microstructure of otoliths of 0+ snapper captured in trawl surveys in 2006, 2007 and 2008.

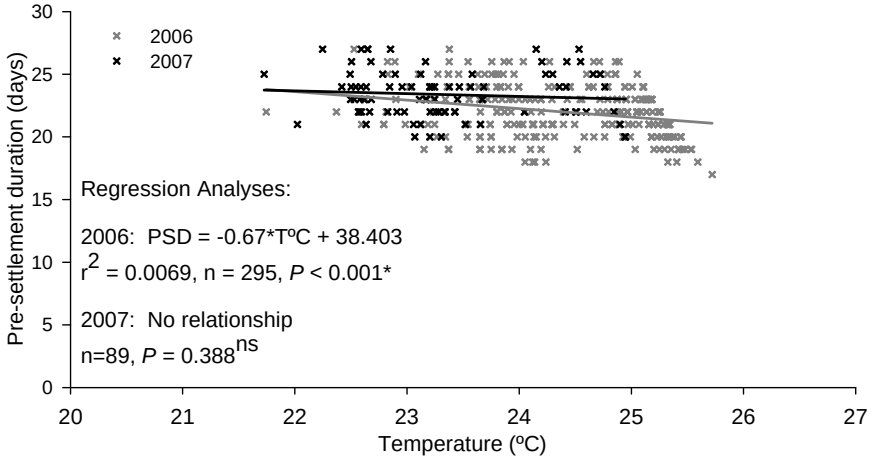


Figure 5.9. Regression analyses of pre-settlement duration and average temperature during the pre-settlement period for 0+ snapper collected in 2006 and 2007.

5.4 Discussion

5.4.1 Inter-annual recruitment variation

The variation in year-class strength observed for snapper in northern Spencer Gulf is large (McGlennon *et al.* 2000; Fowler *et al.* 2007) and is likely to be driven by the inter-annual variation in abundance of 0+ recruits (Fowler and Jennings 2003). In April 2006, the highest abundances of 0+ recruits ever observed in the study were recorded. The following year these abundances were approximately 1/3 the magnitude and in 2008, only three 0+ recruits were captured. Inter-annual variation of a similar magnitude has been observed for snapper previously in New Zealand (Francis 1995) and South Australia (Fowler and Jennings 2003) and is common in other teleosts (see Wright and Bailey 1996; Lapolla and Buckley 2005). There were, however, not only inter-annual differences in the abundances of 0+ recruits captured but considerable inter-annual differences in the timing of spawning of these recruits. Furthermore, there was also considerable variation in the distribution of spawn dates within seasons. Such inter- and intra- annual differences in the timing of successful spawning occur commonly in fish populations and result from a variety of biological and/or physical parameters (Methot 1983; Wright and Bailey 1996; Vinagre *et al.* 2008).

5.4.2 Does spawning affect recruitment?

Observations about spawning of snapper were made during the three seasons considered in this study (Chapter III). Whilst egg production could not be precisely determined on a day to day basis, high rates of spawning activity were recorded throughout December and much of January in 2005/06 and 2006/07. In 2007/08, most spawning occurred in December, but

reproductive activity differed considerably to the two previous years in that more eggs were produced per spawning event, but spawning events were less frequent and over a shorter period. No 0+ snapper spawned in December 2007 were collected in the trawl survey of April 2008 indicating that the major spawning period resulted in no successful recruitment.

The period of spawning that led to successful recruitment, as inferred from back calculated spawn dates, was long, particularly for the 2005/06 season. However, in all three seasons very few 0+ recruits originated from late November and the first week of December. In spite of this, a high rate of spawning was observed for the first week of December, particularly in 2005 and 2006. Some 0+ snapper caught in northern Spencer Gulf were also spawned from February in 2005/06. This contrasted with observations of spawning fish in the region because adult snapper had ceased to spawn by mid to late January in that year. Thus, it is likely that the fish spawned in February 2006 originated from spawning events outside northern Spencer Gulf. This indicated that nursery grounds in northern Spencer Gulf are important not only for locally spawned fish but also for a larger population. The results for 2006/07 differed from the previous season in that no 0+ recruits originated from February and the numbers of recruits from December/January was considerably less. The spread of spawn dates in 2006/07 was entirely encompassed by observations of spawning in that season. In the final season, 2007/08, none of the 3 0+ fish collected came from the time when spawning fish were observed in northern Spencer Gulf, again suggesting that a non-local source contributes 0+ recruits to northern Spencer Gulf nursery grounds. Thus, observations of spawning can explain only part of the recruitment patterns of 0+ snapper. Importantly, the possibility that spawning output controls the various finer scale modes observed in the frequency distributions of spawn dates in the first two seasons cannot be discounted because spawning observations were not precise enough to estimate output on a day-to-day basis. That large periods of egg production resulted in no recruitment indicates that much of the inter- and intra- annual recruitment variation must result from factors other than egg production.

The observation that considerable parts of spawning seasons do not contribute to recruitment has been made for many species of fish (Methot 1983; Allman and Grimes 2002; Lapolla and Buckley 2005; Wright and Gibb 2005; Nishimura *et al.* 2007; Secor 2007). In fact, long spawning seasons and multiple batch spawning may have evolved as a way to expose at least some offspring to conditions suitable for recruitment each year (Winemiller and Rose 1993). A comparison between the reproductive strategy of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) indicated that cod, with the longer spawning season, had less variable recruitment (Fogarty *et al.* 2001). This has important implications for snapper because the spawning season in northern Spencer Gulf is short compared to that for snapper

in other regions (Chapter III). Thus, the window of opportunity for successful recruitment is more limited. However, the effect of spawning on recruitment remains obscure for many species. Rarely has egg production been shown to affect recruitment (but see Myers and Barrowman 1996). In some species, however, settlement patterns do reflect spawning patterns (e.g. Robertson *et al.* 1999), and for many species in different environments, spawning activity varies considerably both within and between seasons (Hunter *et al.* 1985; DeMartini 1991). However, variable mortality and variable larval duration can result in decoupling of spawning and settlement patterns (Danilowicz and Sale 1999; Robertson *et al.* 1999). In the case of snapper in northern Spencer Gulf, the decoupling of spawning patterns, observed from analysis of ovaries in adults, and the timing of successful spawning measured by back-calculation of spawn dates of otoliths of 0+ fish, suggests that mortality during the early life history is a key process that determines the timing and magnitude of successful recruitment.

5.4.3 Lunar and tidal effects on the timing of spawning and settlement

There were several lines of evidence that suggested that recruitment was related to moon phase. In particular, Rayleigh's test indicated that the spawn dates were not distributed evenly through a lunar cycle in either 2005/06 or 2006/07. This was supported for 2005/06 by the autocorrelation analysis, but not for 2006/07. In both these seasons, the strongest recruitment resulted from spawning on the lunar quarters. This effect could result from changes in spawning intensity, fertilisation success or mortality rates that are mediated by lunar phase. Spawning varies according to lunar phase in many fish (Rhodes and Sadovy 2002a,b; Findlay and Allen 2002; Gladstone 2007) but without daily observations of spawning throughout the lunar cycle, this cannot be tested. The frequency distributions of spawn and settlement dates, however, are the same shape and this means that the shape of the distributions may not be set at spawning but, rather, at settlement. Settlement is timed to particular lunar phases in some fish (e.g. Robertson *et al.* 1988; Sponaugle and Pinkhard 2004) but mortality rates also change at the time of settlement such that it can have a significant effect on recruitment (Kaufmann *et al.* 1992).

5.4.4 The impact of temperature on recruitment

The majority of successful spawning of snapper occurred in December and January of 2005/06 and 2006/07, when water temperatures were high, but not at their peak. The timing of spawning in snapper in northern Spencer Gulf exposed offspring to some of the warmest waters available anywhere in South Australia's coastal waters during their larval and early post-settlement life.

Greatest recruitment of 0+ snapper occurred from spawn events on days when temperatures were above 21ºC, which did not occur until early December 2005 or mid-December 2006. This is consistent with an earlier study for the region (Fowler and Jennings 2003). The period above this temperature that coincides with spawning is important to recruitment. However, the 2007/08 season breached this threshold temperature early and the spawning period was concurrent with suitable water temperatures, but resulted in no recruitment. Thus, whilst water temperature was important it was clearly not the only factor that affected recruitment.

Viable snapper larvae have been produced by aquaculture processes in water temperatures from 14 to 25.6ºC, with optimal conditions for survival recorded between 15 and 22 ºC (Foscarini 1988). The temperature range identified in the northern Spencer Gulf was more restricted, with no spawning occurring until temperatures were over 19ºC (Chapter III) and peaks in recruitment resultant from days over 21ºC. The inconsistency between the results from the aquaculture studies and observations from the wild also suggest other factors may play a role.

This, however, only considers the impact of water temperature at the time of spawning and it can have an impact throughout the early life history. For example, sub-optimal temperatures that cause slower growth rates can increase the pre-settlement duration resulting in longer exposure of larvae to high predation rates (Houde 1987). Furthermore, recruitment of snapper and the impact of water temperature have been considered closely in New Zealand (Francis 1993; Francis *et al.*1997). There, the average temperature in the early part of the 0+ year was related to the abundance of the cohorts in their 1+ year observed in trawl surveys. A cumulative effect of temperature on different stages of the early life history was a possible mechanism for the strong relationship reported.

5.4.5 Pre-settlement duration

Pre-settlement period (larval duration) is variable in many fish species. For snapper, considerable variation in pre-settlement period has been observed both in Australia (Fowler and Jennings 2003; this chapter) and New Zealand (Francis 1994a). In the New Zealand study the variation in the length of the pre-settlement period (determined from otolith microstructure) was explained by differences in water temperature, with higher water temperatures resulting in shorter pre-settlement periods. The differences observed in the first three years of this study were thought to relate to water temperature (Fowler and Jennings 2003). In contrast, the relationship between the length of the pre-settlement period and temperature determined in the present study was extremely weak. Similarly, water temperature and somatic growth during the larval phase was also unrelated (Chapter IV). The

evidence indicates that pre-settlement growth of snapper in northern Spencer Gulf was not limited by temperature during the 2005/06 and 2006/07 seasons. The average water temperatures during the pre-settlement period were considerably higher in this study than for those in New Zealand (Francis 1994a). In fact, the temperatures observed in this study were at or beyond the upper limits of those observed in New Zealand. A similar comparison is evident in the relationships between spawning and water temperature between New Zealand and northern Spencer Gulf in that temperatures coincident with spawning were considerably higher in the northern Spencer Gulf than in New Zealand (Chapter III; Francis 1994a). The strong relationship observed between recruitment rate and temperature in New Zealand (Francis 1993; Francis *et al.*1997) is not evident for northern Spencer Gulf. This difference may be a result of the higher temperatures that occur annually in northern Spencer Gulf and suggest temperature has not limited growth or recruitment in the years observed during this study.

There may, however, be a relationship between the pre-settlement duration and year-class strength. In an earlier study, the year with weakest recruitment was made up of fish with relatively long larval durations and the years with stronger recruitment had a broad distribution of larval durations (Fowler and Jennings 2003). In this study the pattern has continued. In 2006, the year with strongest recruitment, a considerable proportion of the 0+ recruits collected had shorter pre-settlement durations than was the case for the following weaker recruitment years. This observation fits with the stage-duration hypothesis (Houde 1987) but importantly we have not linked short larval duration and warmer water.

5.4.6 Conclusions

This study suggests that some of the variation in spawning success is related to temperature and that lunar phase can mediate spawn and settlement date frequencies in snapper. However, intra-annual variation in the strength of 0+ recruitment was not controlled wholly by temperature because the spawning season of 2007/08 resulted in no recruitment in spite of considerable egg production during the period temperatures were within the suitable range as measured in the previous two years. Furthermore, spawning is not a primary determinant of successful recruitment as large portions of egg production resulted in no recruitment in all years. Mortality processes in the egg and larval phase of snapper need to be studied in order to gain more insight into recruitment dynamics of the species.

Chapter VI

The use of food resources by 0+ snapper, *Chrysophrys auratus*, from northern Spencer Gulf; South Australia

6.1 Introduction

The abundance of 0+ fish can differ substantially between habitats as a function of their suitability as nursery areas. Food availability is one factor, amongst many interacting abiotic and biotic influences, that can influence the value of a nursery habitat (Beck *et al.* 2001). Theoretically, areas with greater abundance of food could support juveniles at higher densities and/or provide the necessary resources to increase growth rate (e.g. Jones 1986), thereby reducing susceptibility to predation (Houde 1987). Thus, food availability can be an important determinant of post-settlement mortality to juvenile fish (e.g. Jenkins *et al.* 1996). Food availability, however, is impossible to determine in the absence of an understanding of the diet of a species.

The diet of wild 0+ snapper (C*hrysophrys auratus*) has not been studied in Australia. In Japan, however, it has been considered an important determinant of the distribution and abundance patterns observed in Shijiki Bay (Tanaka 1985). In that case, the gradient of copepod distribution was considered to lead 0+ snapper to nursery areas in the inner parts of the bay where they then switched to feeding on abundant gammaridean amphipods. In New Zealand, food availability has also been implicated in distribution patterns, with juvenile snapper aggregating selectively at sites that provide optimal feeding conditions (Francis 1997). In Australia, the effect of food availability and diet for 0+ snapper has remained the subject of speculation. Hamer and Jenkins (2004) hypothesised that the variety of habitats that 0+ snapper utilise in Victoria may result from variation in prey availability. In South Australia, the association between 0+ snapper and soft sediment environments has been suggested to result from either regional hydrodynamics or dietary influences (Fowler and Jennings 2003).

Trawl surveys done in South Australia's northern Spencer Gulf have identified one small area near Western Shoal (Fig. 6.1) as an important nursery area for 0+ snapper. The area has

consistently supported the highest densities of 0+ snapper observed in the region (Chapter III; Fowler & Jennings 2003). This area is 10 to 25 m deep over unvegetated bottom (Chapters III and V) with fine grained sediment (Fowler and Jennings 2003). The reason it supports higher densities of 0+ snapper than nearby areas is unknown but, given the lack of structural variation and the consequent lack of protection this habitat appears to offer, it is possible that food availability is an important factor.

The general aim of the work described in this chapter was to determine the diet of 0+ snapper in northern Spencer Gulf, South Australia. The specific objectives were to determine if there were annual differences in the prey assemblages taken by 0+ snapper and/or differences between the prey assemblages taken by fish collected in the major nursery area at Western Shoal and those from the other parts of northern Spencer Gulf.

6.2 Methods

6.2.1 Sample collection

Two vessels using different bottom trawls were used to collect 0+ snapper from northern Spencer Gulf. A beam trawl net was towed with the RV Odyssey, a 7 m shark cat, and an otter trawl net from the RV Ngerin, a 26 m trawler. All sampling was done at night in late summer and autumn of 2006 and 2007. (The sampling regimes are described in detail in Chapter III).

6.2.2 Laboratory processing

All 0+ snapper collected in the trawls were measured for caudal fork length (CFL) from the tip of the snout to the posterior end of the middle caudal rays to the nearest mm, and body weight (BW) recorded to the nearest 0.01 g. The stomach from each fish was removed and preserved in 70% ethanol. At a later date, each stomach was removed from the ethanol and opened with a lateral incision under a dissecting microscope at 10x magnification and the contents scraped into a small petri dish. The contents were sorted into the lowest taxonomic levels possible and each taxon was then weighed to the nearest 0.1mg on a Sartorius™ balance. The sum of these weights was calculated and used as total stomach content weight (SCW). If the individual prey items could be distinguished they were also counted.

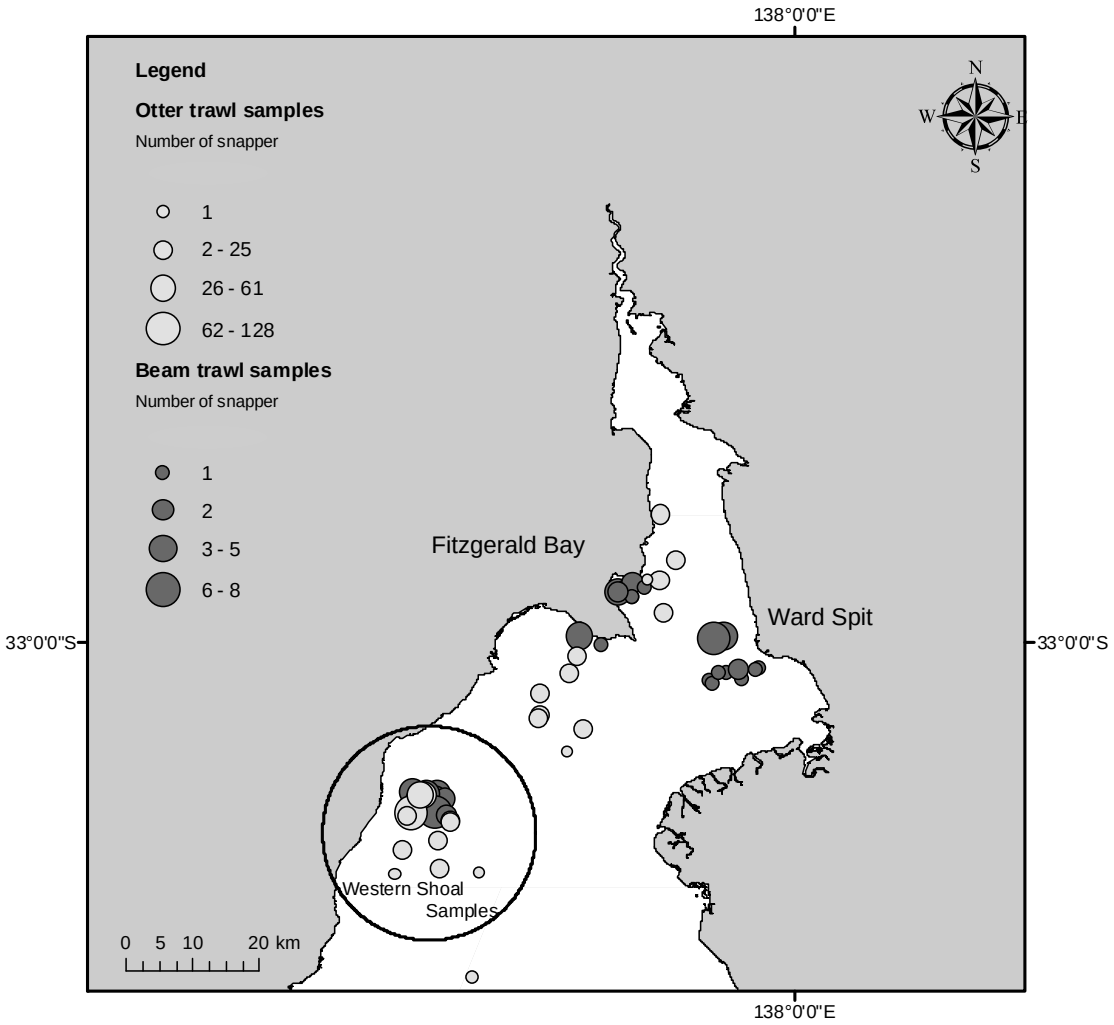


Figure 6.1. Map of northern Spencer Gulf showing the major nursery area, Western Shoal, and the locations and numbers of snapper caught in the beam and otter trawls done in 2006 and 2007. Note that the abundance data for the two nets are in different scales. Samples from the area encircled were classified as having come from Western Shoal. Trawls that contained no catch of 0+ snapper are not illustrated.

6.2.3 Prey identification

Prey identification was done under a dissecting microscope from 10 to 40x magnification. Hard parts, including otoliths, crustacean exoskeletons and polychaete setae, were used to determine presence and, if possible, number of prey items. Occasionally whole prey or near whole prey were present, such as some cephalopods and polychaetes, and these were identified using several different texts (Shepherd and Thomas 1982; Reid and Norman 2000; Poore 2004). Otoliths were identified by comparisons with material from known specimens held at SARDI Aquatic Sciences and/or published descriptions (Furlani *et al.* 2008).

6.2.4 Data treatment and analysis

The weight of the stomach contents relative to body weight (Fullness Weight Index, FWI; Rasero *et al.* 1996) was calculated as: FWI = SCW x 100/ (BW – SCW). Comparisons of

FWI among year and time of day (fixed factors) were made by an orthogonal two factor analysis of variance (ANOVA). For this analysis, samples were categorised into six 2 hour time brackets from sunset, reflecting when fish were captured.

The percentage of empty stomachs was calculated for all trawl stations where catch was $n \geq 3$ and plotted against time of capture. Time of capture was expressed as minutes after sunset. The relationship between time of capture and proportion of empty stomachs was considered by regression analysis.

Three major prey groups were identified: polychaetes, crustaceans and teleosts, but a considerable portion of the stomach contents could not be identified. The percentage of 0+ snapper that contained each of the major prey groups was determined and is reported as percent frequency of occurrence (%FOO). The percentage contribution that each prey group made to the total weight of the stomach contents was also calculated for each fish and is reported as percent contribution (%C).

Non-parametric multivariate techniques from the PRIMER package were used to determine differences in diet according to fish size, location and year.

To determine if the prey assemblage differed depending on the size of the fish sampled, fish were categorised into 10 mm size classes from 20 mm to 100 mm CFL. The percent contribution (%C) of the major prey groups (polychaetes, crustacean, teleosts and unidentified) was used to create a Bray-Curtis Similarity Matrix (Clarke 1993). Data were viewed graphically as a non metric multidimensional scaling (nMDS) ordination. To determine if there were significant differences in the prey assemblage of different size classes of 0+ snapper a one factor analysis of similarity (ANOSIM) was used.

The differences in the prey assemblages of 0+ snapper were considered between years and locations (Western Shoal and elsewhere). The abundance data for the major prey groups were 4^{th} root transformed and a Bray-Curtis Similarity Matrix was computed (Clarke 1993). An nMDS ordination and ANOSIM was then used to consider differences in prey assemblage between years and locations. The relative contributions of the prey groups to the differences detected were then determined using similarity percentages (SIMPER) analysis.

6.3 Results

6.3.1 General information

The 0+ snapper analysed for stomach contents varied between 20 and 101 mm CFL with an average (±s.e.) of 56.93±0.87 mm. A total of 347 preserved stomachs were processed of which 255 (73%) contained prey items. Most of the stomachs that contained prey came from a small region around Western Shoal (Fig. 6.1). Most of the remaining stomachs that contained prey (n=49) were from fish captured north of Western Shoal, particularly around Fitzgerald Bay and Ward Spit (Fig. 6.1). Prey items were usually very well masticated and could only be identified by their hard remains. Identification was therefore generally poor and very few prey items could be identified to species. It was clear that 0+ snapper did not swallow prey whole unless they were very small such as copepods to 2 mm long. Three major prey groups were identified; these were polychaetes, crustaceans and teleosts. A considerable portion of the stomach contents was unidentifiable.

Polychaetes

Polychaetes contributed the most prey biomass of any group (Table 6.1). In total, 136 stomachs contained polychaetes representing 39.5% of all stomachs processed and 53.3% of stomachs that contained prey. Stomachs often contained polychaetes which were usually identified from setae (Fig. 6.2). No whole polychaetes were found and only four stomachs contained polychaete specimens sufficiently intact to identify to genus. These were a nereid polychaete, *Nereis* sp. (Fig. 6.2).

Teleosts

Teleosts were ranked second by biomass (Table 6.1), but were present in only 26 stomachs, representing 7.5% of all stomachs containing prey. No whole teleosts were found and in most cases, taxa were identified from otoliths (Fig. 6.2), although scales, jaws and gill arches were also used. Three species were distinguished, *Engraulis australis*, *Siphamia cephalotes* and *Nesogobius* sp. Two eggs of *Engraulis australis* were also identified in separate stomachs and were the only fish eggs observed.

Crustaceans

Crustaceans were present in 19.0% of stomachs containing prey, but ranked third by biomass (Table 6.1). A similar biomass of crustaceans was found to that of teleosts. Crustaceans were the most diverse prey group containing a minimum of six species but were likely to have included considerably more. Whole prey items were occasionally observed, including amphipods, copepods and an isopod. These were sufficiently digested to render further taxonomic identification impossible. Brachyuran crabs were also present but none were whole. Only one was sufficiently intact to be identified to genus, i.e. a majid crab, *Schizophrys* sp. Two ostracods were also identified from separate stomachs.

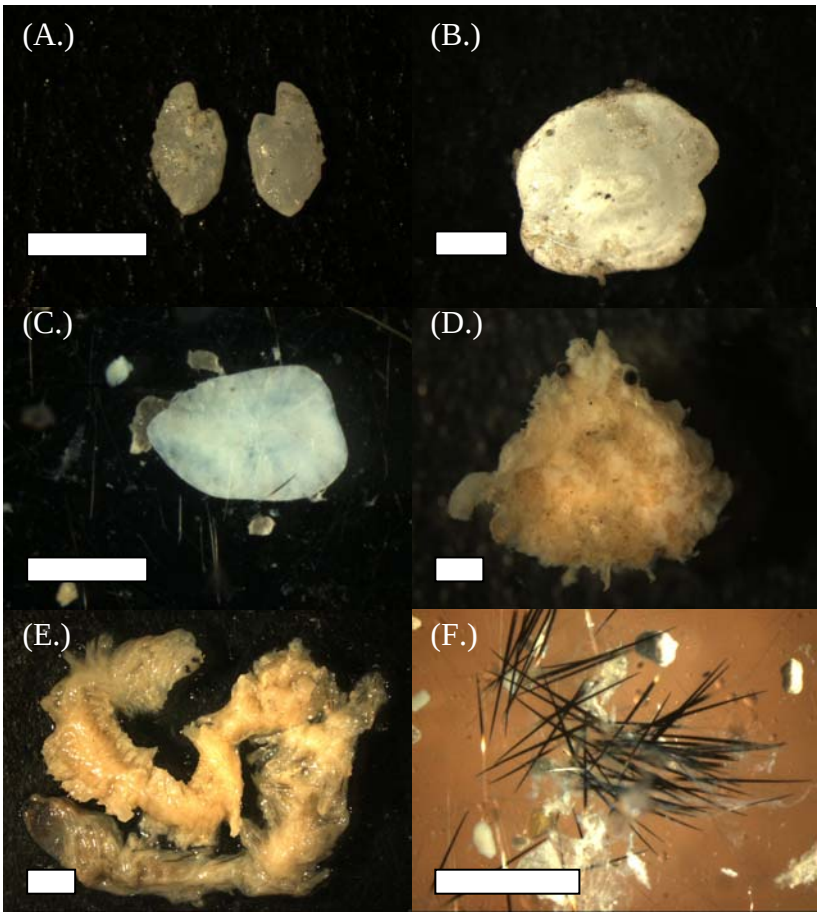


Figure 6.2. Examples of prey remains in the stomachs of 0+ snapper. (A). Otoliths from *Engraulis australis*; (B). Otolith from *Nesogobius* sp.; (C). Otolith from *Siphamia cepalotes*; (D). carapace of *Schizophrys* sp.; (E.) remains of nereid polychaete, probably *Nereis* sp. and (F). setae of polychaetes. Scale bar is 1 mm in all cases.

Table 6.1. Summary of the prey groups found in the stomachs of 0+ snapper collected from northern Spencer Gulf showing frequency of occurrence (FOO%) and total weight of prey items. The centre two columns show a breakdown of the major prey groups to the family or order level and their total weight. The last two columns show a breakdown of the lowest taxonomic level identified for each group and the feature used for identification. Note that the majority of prey items identified to family or order could not be identified to genus or species.

Prey group	FOO %	Total weight (mg)	Family or Group	Weight (mg)	Lowest taxa identified	Method to identify prey
Polychaete	39.5	8591.7	Nereidae	2418.6	*Nereis* spp.	part prey
			unidentified	6173.1		
Crustacea	19.0	2474.1	Amphipoda	82.5	Amphipoda	whole prey
			Copepoda	56.0	Copepoda	whole prey
			Isopoda	26.2	Isopoda	whole prey
			Brachyura	638.9	*Schizophrys* sp.	carapace
			Stomatopoda	62.0	*Belosquilla laevis*	tail fan
			Penaeoidea	298.1	Penaeoidea	part prey
			Caridea	63.5	*Alpheus* spp	claw
			Ostracoda	0.3	Ostracoda	whole prey
			unidentified	1246.6	-	-
Teleost	7.5	2486.4	Clupeidae	-	*Engraulis australis* (egg)	whole prey
				690.4	*Engraulis australis*	otolith
			Apogonidae	165.4	*Siphamia cephalotes*	otolith
			Gobiidae	314.4	*Nesogobius* spp.	otolith
			Unidentified	1316.2	-	-
Mollusca	0.9	161	Cephalopoda	161.0	Octopus	whole prey
			Bivalve	-	Bivalve	part shell
Gastropoda	0.0	-	Gastropoda	-	Gastropoda	part shell
Unidentified	21.6	1349.3	-	-	-	-
Empty stomachs	26.5	-	-	-	-	-

Other prey groups

Unidentified items were present in 21.6% of all stomachs and represented a considerable portion of the biomass (Table 6.1). They were well masticated tissue containing no hard parts. Some identifiable molluscs were present on rare occasions. These were present as lone prey items in individual stomachs and included one gastropod, one bivalve and two octopus (Table 6.1). Collectively these constituted a small prey biomass.

6.3.2 Temporal feeding behaviour

Average FWI was generally higher in samples collected soon after sunset rather than later during the night and early morning (Fig. 3). Time of day significantly affected FWI ($F_{5,336}$ = 2.68 $P<0.001$) and this was consistent for both years ($P>0.05$ for year factor). Post hoc

Tukey's tests also indicated that fish captured earlier in the evening contained more prey (Fig. 6.3).

A greater proportion of stomachs contained prey early in the night than later during the night (Fig. 6.4). The regression was significant and time of day explained 38% of the variance in the proportion of stomachs containing prey (Fig. 6.4).

6.3.3 Prey assemblage

Due to the taxonomic difficulties resulting from the poor quality of specimens retrieved from stomachs, prey assemblages could only be analysed at a broad taxonomic level. Thus, only four major groups were considered in the following analyses; polychaetes, teleosts, crustaceans and unidentified.

Prey assemblages in the stomachs did not vary for different size classes of 0+ snapper (ANOSIM: Global R = -0.014, p = 0.921) (Fig. 6.5, 6). Differences in the prey assemblages taken by 0+ snapper showed little variation between years and locations (Fig. 6.7). A significant difference, however was found between locations (Global R=0.095, p=0.03), but not between years (Global R=-0.013, p= 0.67). The dissimilarity between locations was primarily driven by the high biomass of polychaetes in the diet of those fish collected at Western Shoal (Table 6.2; Fig. 6.8).

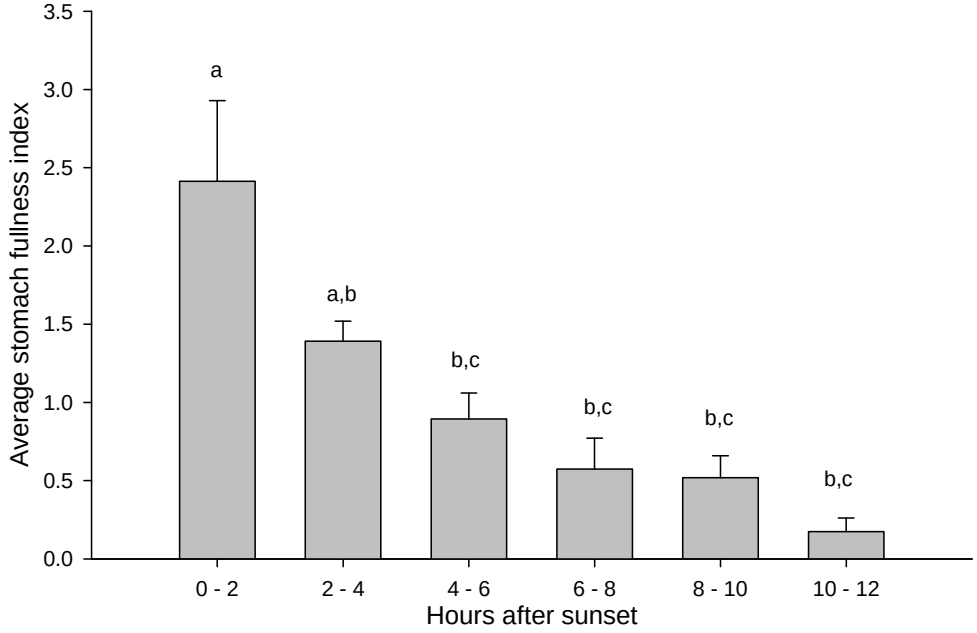


Figure 6.3. Mean FWI (+s.e.) in 2 hour time brackets from sunset. Letters indicate those means not significantly different from each other, as determined by post-hoc tests. (i.e. those that share the same letter are not-significantly different.)

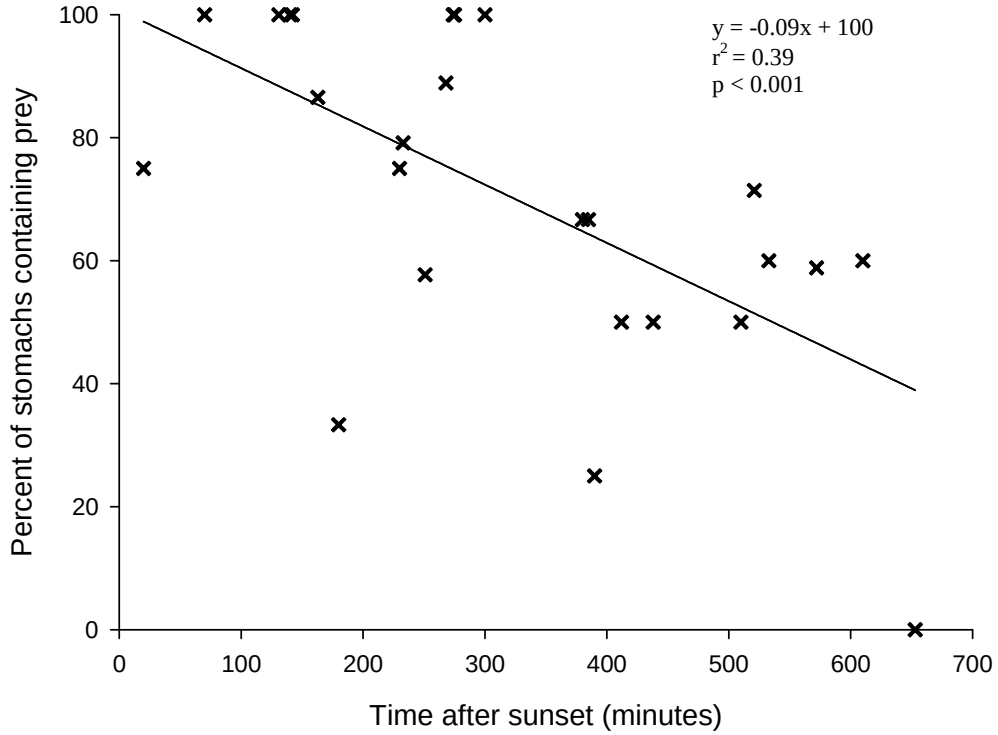


Figure 6.4. Relationship between time after sunset and the proportion of empty stomachs in a trawl sample for catch n≥3. Results of the regression analysis are provided on the figure.

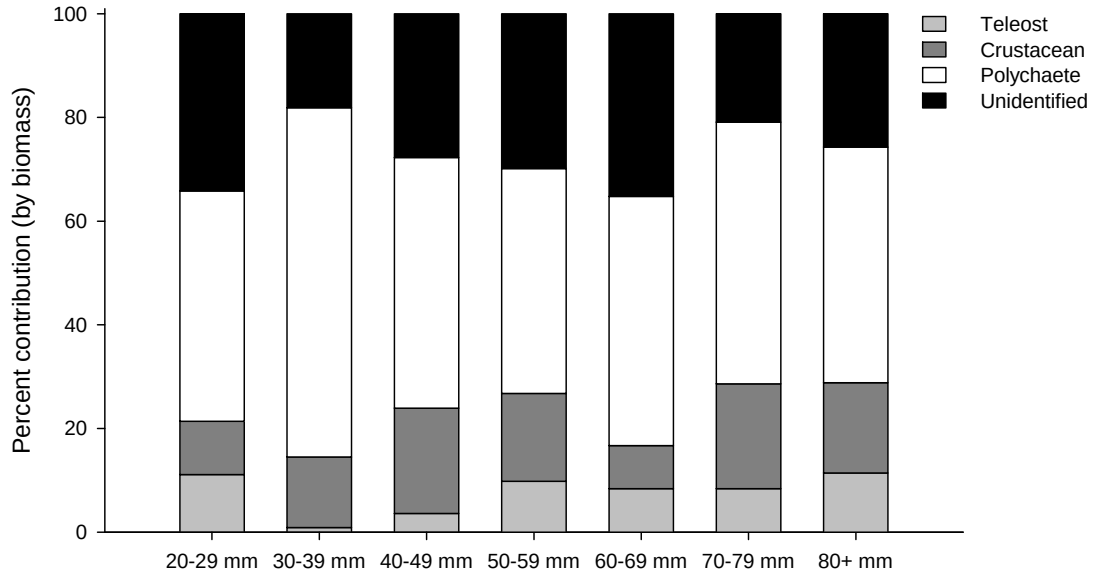


Figure 6.5. Percent contribution of each of the major prey groups calculated from biomass data for different size classes of 0+ snapper. Sample sizes for each category are shown above each bar.

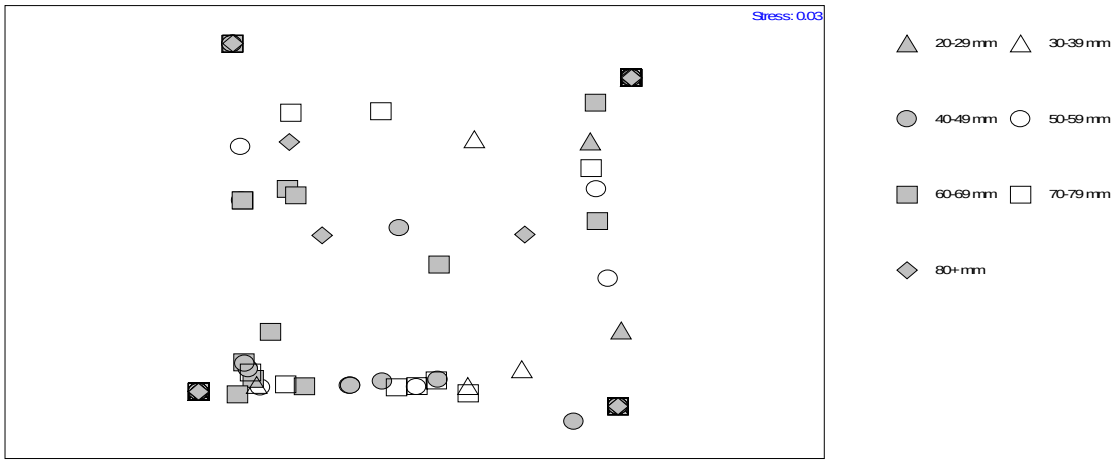


Figure 6.6. Non-metric Multidimensional Scaling ordination calculated from a Bray-Curtis similarity matrix derived from the proportional contribution of prey group biomass to total prey biomass for each 0+ snapper containing prey. Stress = 0.03 Fish are categorised into six ten mm size classes and one over 80 mm size class.

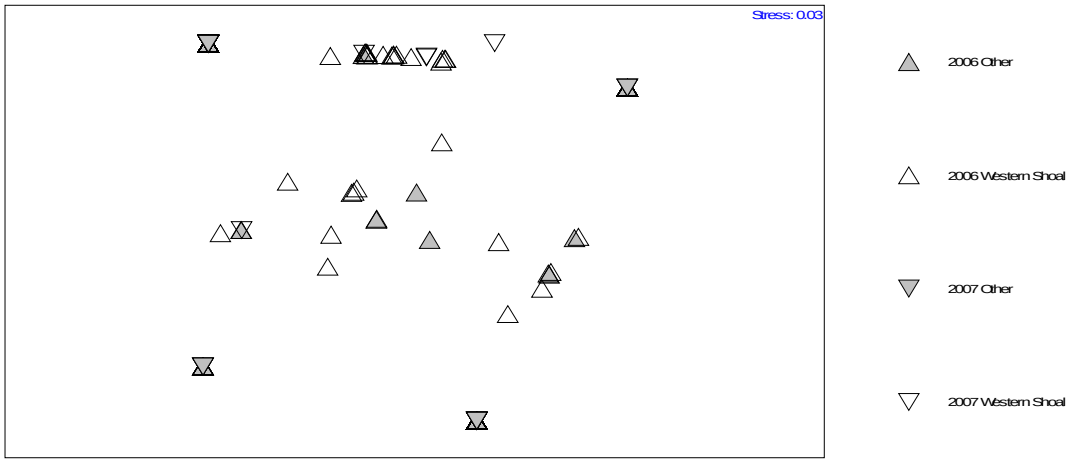


Figure 6.7. Non-metric multidimensional scaling ordination of prey biomass in 0+ snapper that contained prey. Stress = 0.03. Symbols distinguish the location and year that samples were collected.

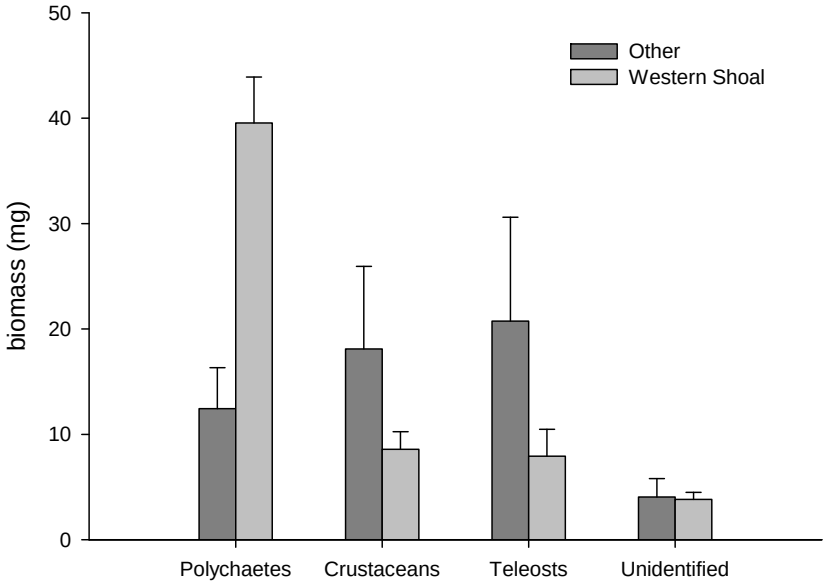


Figure 6.8. Biomass of major prey categories identified in stomach contents of 0+ snapper from Western Shoal and those collected from elsewhere in northern Spencer Gulf. Error bars are standard errors.

Table 6.2. Results from the SIMPER analysis indicating the contribution of different prey groups to the difference between stomach contents of fish from Western Shoal and other areas of northern Spencer Gulf.

Prey Group	Mean biomass (mg) Western Shoal	Mean biomass (mg) other areas of NSG	Contribution (%)	Cumulative (%)
Polychaeta	39.56	12.43	34.7	34.7
Unidentified	3.84	4.05	28.9	63.6
Crustacea	8.57	18.09	25.0	88.6
Teleosts	7.92	20.74	11.4	100.

6.4 Discussion

The 0+ snapper, like other juvenile sparids, is an opportunistic and carnivorous feeder that utilised food resources from a wide array of taxonomic groups (Castriota *et al.* 2006; Derbal *et al.* 2007). In snapper, unlike other juvenile sparids, polychaetes contributed most by biomass and by frequency of occurrence. Only specimens from four stomachs could be identified to genus, namely *Nereis* sp. Generally polychaetes were recognised in the stomachs from the setae which remained intact after ingestion but these were not sufficient to identify the worms even to family. Previously, polychaetes have been reported as an important contributor to the diet of small snapper (<10 cm) from New Zealand and similar taxonomic difficulties were also encountered in that work (Godfriaux 1969).

Stomachs were fullest in early evening suggesting that 0+ snapper fed during daylight hours or early darkness. A similar feeding pattern has been observed in New Zealand (Francis 1997) and Japan (Azeta *et al.* 1980b; Sudo *et al.* 1987). This explains some of the difficulties in identification because, particularly for soft bodied organisms, digestion would be rapid. In future, sampling for dietary analysis of 0+ snapper should be altered to include sampling during daylight hours, although sampling effort would need to be significantly increased to counter the effect of net avoidance.

Small crustaceans including amphipods and copepods were sometimes taken whole but larger crustaceans, such as brachyurans, were rarely whole. Often only appendages were present suggesting a preference or capability for taking only part of a prey item. This is a phenomenon recognised for other 0+ fishes, such as *Hippoglossus stenolepis* (Hardman and Southward *in* Holladay and Norcross 1995) which utilise decapod appendages rather than the whole prey. Taking only part prey items and the damage to prey caused by the dentition meant that numerical abundance was not a suitable method for determining the diet of 0+ snapper.

Teleosts were a regular component of the diet of 0+ snapper, particularly otoliths of *Nesogobius*. This genus was found regularly as by-catch in the trawls that targeted 0+ snapper (Chapter VII). Other fishes encountered included *Engraulis australis*, which was also a common component of the trawl by-catch and a single *Siphamia cephalotes*, also extremely abundant in northern Spencer Gulf. Interestingly, the most common, small-bodied benthic fish in northern Spencer Gulf, the pinguipedid, *Parapercis haackei* (Chapter VII), was never encountered in the stomachs of 0+ snapper.

Even at a general taxonomic level, a difference between the major nursery area at Western Shoal and the remaining parts of northern Spencer Gulf was detected. Spatial variability in diet is common among fish (Edgar and Shaw 1995) and has been observed for 0+ snapper in Shijiki Bay, Japan (Tanaka 1985). There, small crustaceans such as amphipods and copepods were numerically very important components of the diet (Sudo & Azeta 2001; Tanaka 1985), but copepod prey became more important further from the head of the bay (Tanaka 1985). In fact, it was proposed that snapper were guided by an increasing abundance of copepod prey toward shallow *Zostera* beds, which they then utilised as nursery areas. When they reached these *Zostera* beds, they switched to feeding on the abundant gammaridean amphipods that occurred there (Sudo & Azeta 2001). The 0+ snapper in Shijiki Bay also ate polychaetes, fish eggs, arrow worms and mysid shrimps (Tanaka 1985), but no biomass information was available. The demersal juveniles considered in the Japanese studies were small, i.e. mostly less than 30 mm CFL (Tanaka 1985). The 0+ snapper from northern Spencer Gulf analysed for stomach content were generally larger, making comparisons difficult. The dominance of polychaetes and rarity of whole prey suggests a different feeding strategy to that of the smaller fish examined from Japan. Whether this difference was ontogenetic or related to the study locations is not known. That no differences in the prey assemblage taken by different size classes of snapper were detected for northern Spencer Gulf may reflect the broad taxonomic categories. For example, prey such as copepods, amphipods and decapods were pooled together as crustaceans for the analysis, due to the large portion of unidentified crustaceans in stomachs. This indicates that to determine ontogenetic changes in diet would require more precise taxonomy which could be provided using molecular dietary analysis techniques (see Sigler *et al.* 2006; Casper *et al.* 2007).

The current state of knowledge of distribution of polychaetes in northern Spencer Gulf is insufficient to address questions of diet selectivity. The literature on the distribution of Nereidae from Spencer Gulf indicates that habitat use is species specific (Hutchings *et al.* 1993). Identification of the polychaete species that snapper prey upon remains unresolved which prevents further consideration of their life histories or the habitats they occupy.

The relatively high abundance of polychaetes in stomachs of 0+ snapper from Western Shoal compared to the remaining parts of northern Spencer Gulf gave an indication that food availability may be an important determinant of 0+ densities and is likely to influence the value of Western Shoal as a nursery area. However, many interacting abiotic and biotic factors influence the value of nursery areas (Beck *et al.* 2001) and processes underlying the delivery and/or survival of 0+ snapper or their active selection of the nursery area at Western Shoal are unknown. Thus, whilst differences in diet of the snapper collected from Western

Shoal to elsewhere in northern Spencer Gulf suggests that the available resources are different but it may not be a causative relationship. Until factors such as the rate of larval delivery and predation can be determined for different areas in northern Spencer Gulf, the reasons Western Shoal supports a consistently high density of 0+ snapper remain speculative.

Chapter VII

The trawl assemblages of northern Spencer Gulf and the associations of 0+ snapper, *Chrysophrys auratus*

7.1 Introduction

Physical and biological factors that influence larval settlement, growth and survival have a considerable impact on the value of habitats as nursery areas (Beck *et al.* 2001; 2003). The degree to which juveniles are obligate or facultative in terms of their habitat requirements varies between and within species (Adams *et al.* 2006), but in broadcast spawning fishes, a high level of habitat specificity immediately post-settlement is often observed (Langton *et al.* 1996). The amount and relative contribution of juvenile fish from different nursery habitats to the adult population can have considerable implications for the dynamics of fish populations. The contribution of juveniles from various nursery habitats to the adult population is particularly important if the rate of mortality of juveniles differs between nursery areas.

The ability to identify areas of high juvenile abundance and their habitat associations can make significant contributions to successful conservation and management (Juanes 2007). It is challenging to determine habitat associations and to identify nursery areas, because this is often complicated by variation in recruitment relating to mortality in the egg and larval phases (Houde 1987). As such, the absence of juveniles from a particular area in a given year does not necessarily mean that suitable habitat was unavailable. If the species assemblage(s) that juveniles of a species associate with can be determined, it may be possible to identify their nursery areas even during weak recruitment years. Furthermore, it is possible to determine habitat distributions from the presence or absence of different species assemblages (Auster *et al.* 2001). Thus, assemblage structure could provide useful data on likely distribution and habitat associations of different life history stages of commercially important species.

Snapper (*Chrysophrys auratus*), is a large sparid that supports fishing industries in New Zealand, Australia and Japan. Soft sediment bottom is an important habitat type for 0+ year-classes of snapper (Tanaka 1985; Francis 1995) but there have also been reports that 0+ year-

classes utilise estuarine (Ferrell and Sumpton 1998) and reef (Kingett and Choat 1981) environments. In South Australia, the only known nursery areas for 0+ fish are located in northern Spencer Gulf (Fig. 7.1) (Fowler and Jennings 2003; Chapter III) but, given the broad distribution of spawning adults in the State (Fowler *et al.* 2007), it is possible that other important nursery areas exist elsewhere.

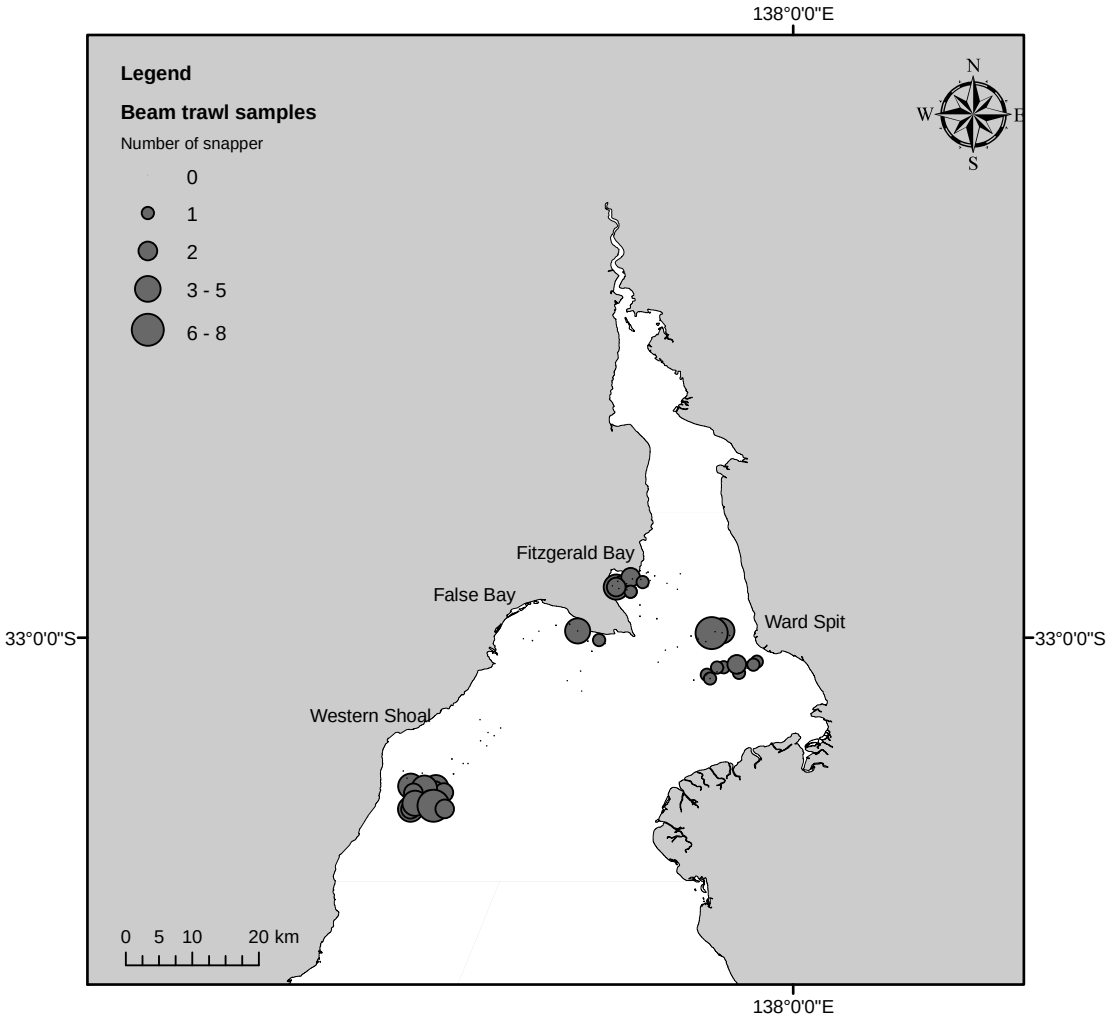


Figure 7.1. Locations of all beam trawls done in 2006 and 2007 and total catch of 0+ snapper.

In northern Spencer Gulf, fish inhabit these nursery areas for only their first year of life. Furthermore, it appears that recruitment either fails, or is extremely poor in most years (Fowler and Jennings 2003; Fowler *et al.* 2005b; Chapter III). Age structure information and trawl surveys for 0+ age classes indicate that strong year-classes occur quite sporadically (Fowler and Jennings 2003; Fowler *et al.* 2007; Chapter III). Thus, the absence of 0+ age classes from a particular area in a given year does not mean that the area does not provide suitable nursery habitat. Currently, the identification of a nursery area would require broad sampling throughout the State's waters in years when strong 0+ age classes have recruited. To identify potential nurseries for 0+ age classes, species that co-occur with them may

provide a useful indicator of where to focus future sampling or efforts to conserve potential nursery habitat. This study was conducted, during two years when recruitment of 0+ snapper was well above average, to describe the assemblage of teleosts and mobile macro-invertebrates that co-occurred with 0+ snapper. This information was then used to identify possible surrogate species so as to determine likely 0+ snapper nursery areas.

The specific aim of this chapter was to describe the teleost and macro-invertebrate community in northern Spencer Gulf, to determine the species that most commonly co-occurred or had discontinuous distributions with snapper, and to identify surrogate species or assemblage structure that was indicative of suitable nursery habitat for 0+ snapper.

7.2 Methods

7.2.1 General

Samples of the benthic assemblage in northern Spencer Gulf were collected by beam trawling. Three sampling trips were undertaken to northern Spencer Gulf in 2006. Four locations, i.e. Fitzgerald Bay, Ward Spit, False Bay and Western Shoal (Fig. 7.1), were selected for sampling on the basis that 0+ snapper had been captured nearby using a different sampling methodology (Fowler and Jennings 2003; Chapters III and V). Trawl shots were allocated haphazardly to each location (Fig. 7.1). The sampling was done in late February to early March and repeated in late March to early April (Table 7.1). The third sampling trip was undertaken in early May 2006 when it became clear that an important 0+ nursery had not been sampled. This third sampling trip involved six shots immediately to the south of Western Shoal (Fig. 7.1).

In 2007, the sampling was altered on the basis of the results of the previous year to improve sampling efficiency. False Bay was excluded from the sampling design and three extra shots were haphazardly assigned to each of the remaining three locations.

7.2.2 Trawl type

A plumb-staff beam trawl with a 3 m beam, 4 mm^2 knotless mesh in the body and 3 mm^2 in the cod end was used in this study. The net was based on the design used to sample juvenile snapper in Port Phillip Bay (Hamer *et al.* 1998; Hamer and Jenkins 2004) with some modifications: a rubber mat was attached to the underside of the cod end to protect the mesh from contact with the bottom; stainless steel cable was used on the lower bridles; a central rope was used to support the beam; and no emergency retrieval line was attached, for ease of deployment. The net was deployed from the RV Odyssey, a 7 m shark-cat, and towed at a

speed of 1.5 to 2 knots. Each trawl had a fixed duration of 5 minutes from when the net made contact with the bottom until initiation of retrieval. Each trawl traversed approximately 300 metres of seabed depending on sea and weather conditions. All sampling was done at night to minimise net avoidance by the fishes.

7.2.3 Species identification and data collection

All teleost fish were identified to species level, counted and weighed. Elasmobranchs were identified to species, counted but not weighed. In 2006, *Penaeus latisulcatus* (western king prawns) were retained, counted and weighed but, due to practical considerations in 2007, they were counted at sea, returned to the water and not weighed. All decapod crabs were identified to species and counted but were not weighed. The remaining crustaceans were identified to species, counted and weighed. All cephalopods were identified to species, counted and weighed except for species of octopus. The octopus could not be identified to species because of the freezing process and damage from the trawl. Thus, they were grouped together in a single multi-species taxon: *Octopus* spp.

Table 7.1. Location and dates of beam trawl sampling trips done in northern Spencer Gulf for which abundance of all fish and motile macro-invertebrates was calculated.

Year	Sampling trip	Location	Number of trawls
2006	Sample trip 1 (27th February to 3rd March)	False Bay	6
		Fitzgerald Bay	8
		Ward Spit	8
		Western Shoal	8
	Sample trip 2 (4th - 6th April and 9th - 10th April)	False Bay	8
		Fitzgerald Bay	8
		Ward Spit	9
		Western Shoal	9
	Sample trip 3 (10th - 11th May)	Western Shoal (s)	6
2007	Sample trip 1 (20th - 23rd February)	Fitzgerald Bay	12
		Ward Spit	12
		Western Shoal	12
	Sample trip 2 (19th - 22nd March)	Fitzgerald Bay	12
		Ward Spit	12
		Western Shoal	12

7.2.4 Data treatment and statistical analyses

The species assemblages that occur in northern Spencer Gulf were described from all trawl surveys. The species collected were ranked according to their numerical abundance and according to their frequency of occurrence in trawl shots across all surveys. Average species richness (alpha diversity) and total number of species (gamma diversity) were calculated for all trawl shots, but 0+ snapper were excluded from these calculations.

Non-parametric multivariate techniques from the PRIMER package were used to determine if trawl shots could be grouped according to the similarity of their assemblages. Total abundances of each species collected were 4^{th} root transformed and a Bray-Curtis similarity matrix was computed (Clarke 1993). Hierarchical agglomerative clustering, using group average linking, was done and the results interpreted from a dendrogram. Differences between clusters were tested using SIMPROF analyses at the 0.01 significance level. On the basis of this analysis, the trawls shots were divided at 25% similarity (the first division in the cluster) into Group A, in which no snapper were captured, and Group B, which sometimes captured snapper. Data were viewed graphically as a non-metric multidimensional scaling (nMDS) ordination. This was used to illustrate the distribution of snapper amongst the two assemblages. SIMPER analysis was used to identify the relative contributions of different species to the differences between the two Groups and similarity within Groups. Species diversity was also compared between Group A and Group B trawls using a t-test.

To determine if the association of 0+ snapper within the Group B assemblage differed a Bray-Curtis similarity matrix was computed from the 4^{th} root transformed abundance data of trawls classified as Group B for sampling trip 2 and 3 in 2006 and sampling trip 2 in 2007. Only Group B trawls were considered because no 0+ snapper were captured in trawls identified as Group A and sampling trip 1 for each year was not used because the timing of these sampling trips meant that not all 0+ snapper that had been spawned had made the transition from the planktonic larvae to post-settlement juveniles at that time. ANOSIM was used to determine whether Group B trawls that contained 0+ snapper differed in the assemblage from those that had no snapper.

7.3 Results

7.3.1 Characteristics of assemblages in northern Spencer Gulf

A total of 142 trawls were done for all sampling times with 29,774 individuals captured and identified. The total number of species encountered was 107 including 77 teleost species, 3 elasmobranchs, 20 crustaceans and 7 cephalopods (including octopus as one taxon) (Appendix 2). The average number of species collected per trawl (±s.e.) was 15.28±0.42.

7.3.2 Abundance

The most abundant species was *Penaeus latisulcatus* (Table 7.2). Two other crustaceans were also very abundant species with *Portunus pelagicus* ranking 3rd and *Metapenaeopsis lindae* ranking 10th across all trawls. The most abundant teleost species was *Parapercis haackei* (ranked 2nd overall), a small bodied pinguipedid. Other abundant species included the pipefish *Stigmatopora argus*, a weed whiting *Siphonognathus radiatus* and the stinkfish *Repomucenus calcaratus* (Table 7.3).

The most frequently encountered species was *Parapercis haackei*, which was captured in 93.6% of trawls (Table 7.3). *Penaeus latisulcatus* and *Portunus pelagicus* were captured in 83.8 and 82.4% of trawls, respectively. *Chrysophrys auratus* was the 29th most abundant species and occurred in 26.8% of all trawls.

7.3.3 Biomass

The biomass data are incomplete because weights could not be recorded for all species. However, the species captured in the highest biomass in 2006 was *Penaeus latisulcatus*. In total, 34.2 kg of *P. latisulcatus* were captured in the 3 sampling trips in 2006 and contributed most to the biomass each trip. No biomass information was collected for *P. latisulcatus* in 2007 because the volume of animals was too large to retain and conditions on board the vessel were unsuitable to weigh the samples accurately.

The 10 species that contributed most to biomass across all sampling trips are listed in Table 7.4, excluding *P. latisulcatus* because these were not weighed in 2007. The highest biomass teleost across all trawls was *Parapercis haackei.* Two larger bodied species (the cepahalopod *Sepia apama* and the teleost *Pseudorhombus jenynsii*) contributed significantly to the biomass across all trawls. *Chrysophrys auratus* ranked 32nd with a total biomass of 274.6 grams.

7.3.4 Assemblage structure

The cluster analysis and associated SIMPROF test indicated two groups of trawls at 25% similarity that were significantly different (Fig. 7.2). No 0+ *Chrysophrys auratus* were captured in trawls classified as Group A whilst not all Group B trawls contained 0+ *Chrysophrys auratus* (Fig. 7.2). The nMDS ordination of the trawl shots illustrates the separation between Group A and B trawls as well as the distribution of 0+ *Chrysophrys auratus* amongst trawl shots (Fig. 7.3). A significant difference in species diversity was also detected. Group B trawls had an average species diversity (±s.e.) of 14.3±0.4, whilst Group A trawls had a species diversity of 17.9±1.1 (t-test: t = 3.495, d.f. = 140, $p = 0.001$).

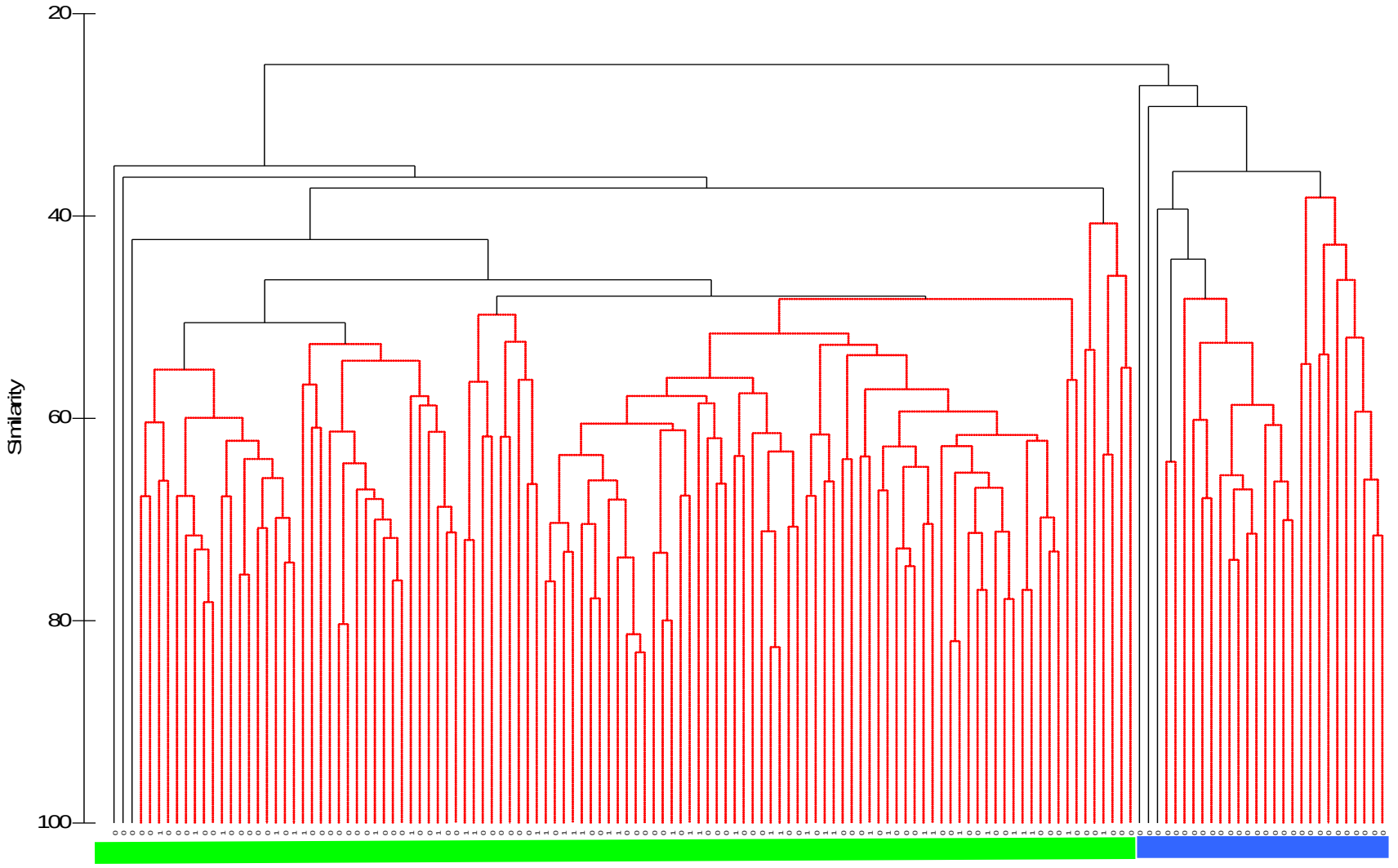
Table 7.2. Ten most abundant species ranked from highest to least by numerical abundance and the rank for snapper (*Chrysophrys auratus*) across all trawls.

Rank	Species	Number	Frequency
1	*Penaeus latisulcatus*	9411	83.8
2	*Parapercis haackei*	4578	93.6
3	*Portunus pelagicus*	1986	82.4
4	*Stigmatopora argus*	1822	21.1
5	*Siphamia cephalotes*	1519	48.6
6	*Siphonognathus radiatus*	1087	12.0
7	*Vincentia conspersa*	1051	58.5
8	*Acanthaluteres spilomelanurus*	1005	54.2
9	*Repomucenus calcaratus*	899	65.5
10	*Metapenaeopsis lindae*	715	31.7
29	*Chrysophrys auratus*	81	26.8

Table 7.3. Ten most abundant species by frequency including the rank and frequency for snapper (*Chrysophrys auratus*).

Rank	Species	Frequency	Rank by numerical abundance
1	*Parapercis haackei*	93.7	2
2	*Penaeus latisulcatus*	83.8	1
3	*Portunus pelagicus*	82.4	3
4	*Repomucenus calcaratus*	65.5	9
5	*Brachaluteres jacksonianus*	62.7	15
6	*Belosquilla laevis*	62.0	11
7	*Vincentia conspersa*	58.5	7
8	*Acanthaluteres spilomelanurus*	54.2	8
9	*Siphamia cephalotes*	48.6	5
10	*Gymnapistes marmoratus*	45.8	14
21	*Chrysophrys auratus*	26.8	29

Figure 7.2. Dendrogram derived using hierarchical agglomerative clustering and group average linking of trawls from all surveys. Two groups that were 25% similar (75% dissimilar) are highlighted below the dendrogrom. All clusters that were not significantly different at the p = 0.01 level are highlighted in red. Group A trawls are highlighted in blue and never contained snapper, and Group B trawls are highlighted in green and sometimes contained 0+ snapper. The presence of snapper in trawls is indicated by 1 and absence by 0.



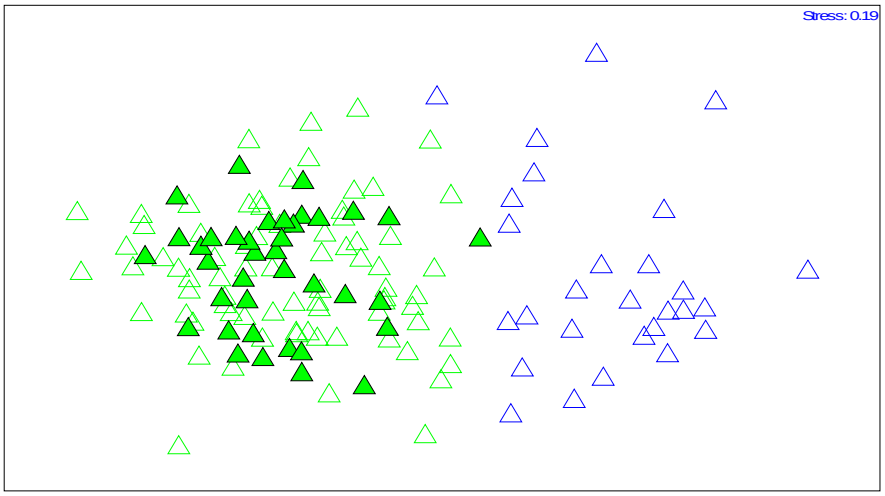


Figure 7.3. Non-Metric multidimensional scaling ordination of the trawls from all sampling trips. Stress = 0.19. Trawls in green are those identified in the Cluster analysis as Group B and those in blue as Group A. Open triangles are stations without snapper and closed stations are those with snapper.

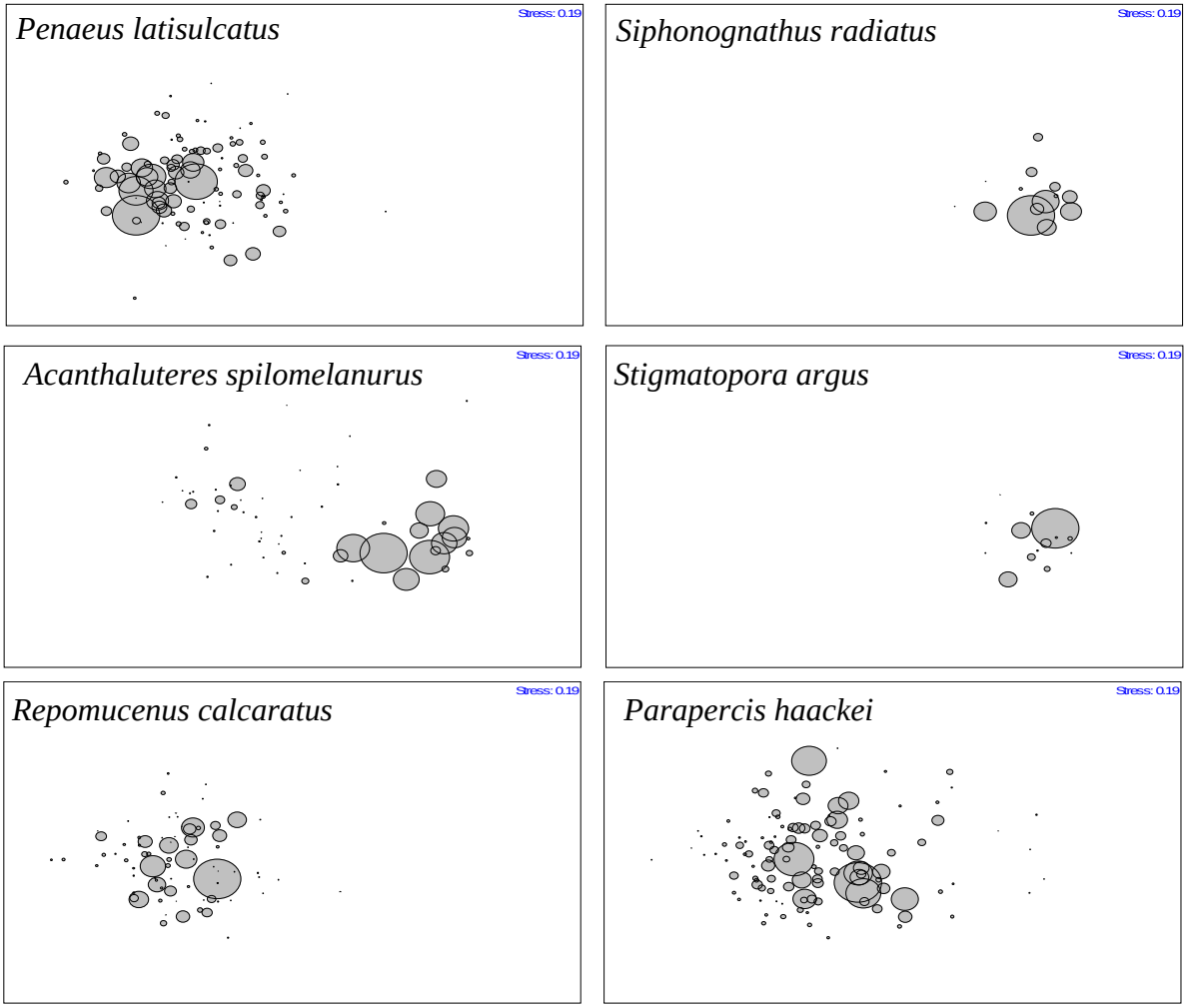


Figure 7.4. Non-metric multidimensional scaling ordination of trawls in species space showing the distribution between groups and abundance of species identified as contributing most to the dissimilarity between Group A and Group B in the SIMPER analysis. Larger circles indicate more individuals and trawls with zero catch are not illustrated. The nMDS plots are the same as that produced in Figure 7.4.

Table 7.4. The ten species contributed most in terms of biomass and the rank for snapper (*Chyrsophrys auratus*) across all trawls. *Penaeus latisulcatus* were excluded because they were only weighed in the first year of sampling.

Rank	Species	Weight (g)	Number of individuals	Average weight (g)
1	*Parapercis haackei*	14673.1	4578	3.2
2	*Sepia apama*	5939.7	26	228.5
3	*Pseudorhombus jenynsii*	4988.8	71	70.3
4	*Acanthaluteres spilomelanurus*	4238.0	1005	4.2
5	*Repomucenus calcaratus*	4180.4	899	4.7
6	*Gymnapistes marmoratus*	3895.6	376	10.4
7	*Siphonognathus radiatus*	3784.5	1087	3.5
8	*Pelates octolineatus*	3779.3	145	26.1
9	*Belosquilla laevis*	3010.0	545	5.5
10	*Vincentia conspersa*	2902.6	1051	2.8
32	*Chrysophrys auratus*	274.6	81	3.4

Species that were abundant in Group A but rare in Group B were *Stigmatopora argus*, *Acanthaluteres spilomelanurus* and *Siphonognathus radiatus*. The latter never occurred in Group B samples. Conversely, *Penaeus latisculcatus* was very common in Group B trawls but rare in Group A trawls. The importance of these species in differentiating the two groups is also seen when their abundances are super-imposed on the nMDS (Figure 7.4).

Group A was characterised by higher abundances of the teleosts *Acanthaluteres spilomelanurus*, *Vincentia conspersa* and *Stigmatopora argus* (Table 7.6a). High abundances of the decapods *Penaeus latisulcatus* and *Portunus pelagicus* and teleost *Parapercis haackei* characterised Group B (Table 7.6b). The teleosts *Repomucenus calcaratus* and *Brachaluteres jacksonianus* as well as the stomatopod *Belosquilla laevis* were also frequently found in Group B trawl shots.

0+ *Chyrsophrys auratus* were captured in 59.3% of Group B trawls done in 2006 and 32.4% in 2007, and in none of the Group A trawls. The nMDS of Group B trawls from sampling trips 2 and 3 in 2006 and trip 2 in 2007 shows that the trawls in which 0+ *Chyrsophrys auratus* were captured overlapped between years, although the majority of trawls were clumped together (Fig. 7.5). The presence of snapper was not associated with any differences in the assemblage within the Group B trawl shots (Global R = -0.014, p = 0.664).

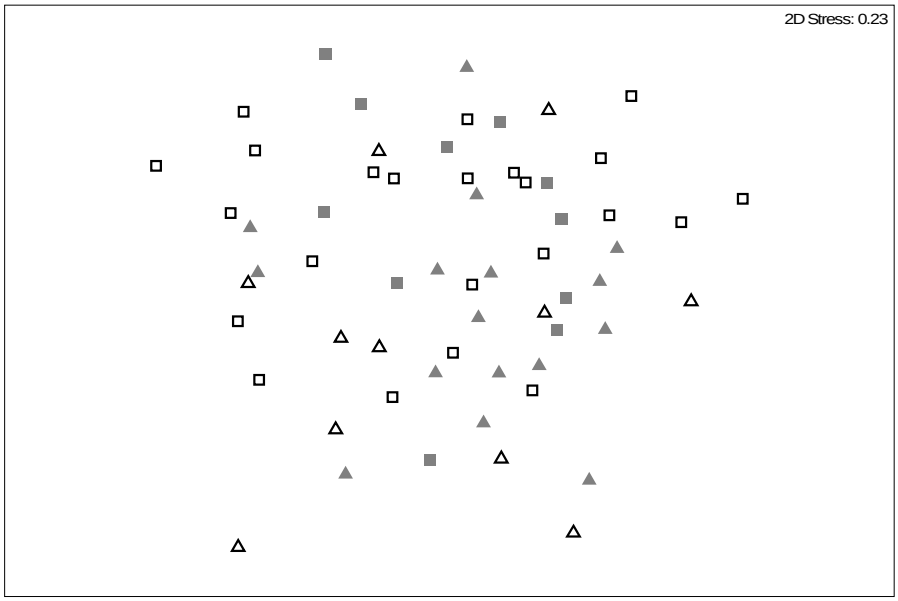


Figure 7.5. Non-Metric multi-dimensional scaling ordination of the Group B trawls from Surveys 2 and 3 in 2006 and Survey 2 in 2007. Stress = 0.23. Triangles are trawls done in 2006 and squares are those done in 2007. Solid shapes are trawls that contained snapper and open shapes are those that did not contain snapper.

Table 7.6. (a.) Results from the SIMPER analysis indicating those species that contributed up to 75% of the similarity between trawls classified as Group A and (b.) the same for those classified as Group B.

(a.)

Species	Mean abundance	Contribution %	Cumulative %
Acanthaluteres spilomelanurus	26.71	13.36	13.36
Vincentia conspersa	22.54	10.77	24.12
Stigmatopora argus	64.39	8.49	32.61
Parapercis haackei	7.86	7.08	39.69
Portunus pelagicus	11.64	6.34	46.04
Upeneichthys vlamingii	4.86	6.17	52.21
Siphonognathus radiatus	38.82	5.8	58.01
Brachaluteres jacksonianus	2.82	5.61	63.61
Scobinichthys granulatus	11.39	4.98	68.59
Vincentia badia	6.79	3.99	72.58
Siphamia cephalotes	10.96	2.99	75.57

(b.)

Species	Mean abundance	Contribution %	Cumulative %
Penaeus latisulcatus	82.31	23.88	23.88
Parapercis haackei	38.23	19.8	43.68
Portunus pelagicus	14.56	10.47	54.15
Repomucenus calcaratus	7.86	8.22	62.37
Belosquilla laevis	4.76	6.79	69.17
Brachaluteres jacksonianus	2.25	3.66	72.83
Vincentia conspersa	3.68	3	75.82

7.4 Discussion

This study has characterised the assemblages of fish and macro-invertebrates in northern Spencer Gulf from beam-trawls. The assemblage of fish and macro-invertebrates that inhabits northern Spencer Gulf is diverse, but is dominated, in terms of numbers, by the crustaceans *Penaeus latisulcatus* and *Portunus pelagicus*. *Penaeus latisulcatus* contributed the highest biomass in the area although it is likely that *Portunus pelagicus* was also important. Whilst the abundance and biomass of these two species of crustaceans were high, the diversity of the crustaceans was relatively low, with only 20 species collected. In contrast, the biomass of fishes was relatively low but diversity was very high, including 77 species. The biology of the most common fish, the grubfish *Parapercis haackei,* is not known but, given its high abundance, it is clearly an important component of the northern Spencer Gulf ecosystem.

7.4.1 Group A and Group B assemblages

Habitat mapping done in northern Spencer Gulf has delineated two broad habitat types: unvegetated soft bottom and seagrass (*Posidonia* spp.) (Edyvane 2000; Bryars 2003). A comparison between these maps and the trawl locations indicated that Group A shots were conducted on seagrass and Group B shots on unvegetated soft bottom (Edyvane 2000; Bryars 2003). This corresponds well with the biology of the species that characterise the Groups. In Group A the most abundant species, the pipefish, *Stigmatopora argus,* and the weed whiting, *Siphonognathus radiatus,* are known to be associated with the seagrasses *Posidonia* spp. (MacArthur and Hyndes 2001; Gomon *et al.* 2008). The habitat associations of the teleost species that characterised Group B are less well known but both the stomatopod *Belosquilla laevis* and decapod *Penaeus latisulcatus* are considered to be species that are found on fine sediment/bare sand, presumably because they both burrow into the substratum (Gowlett-Holmes 2008). The characterisation of Group B was mainly on the basis of higher abundances of *Penaeus latisulcatus*, *Portunus pelagicus* and *Parapercis haackei*. These species were also captured in Group A trawls but in lower abundances. This is because either these species are not obligate to a particular habitat, or different size individuals are found over different habitats, or that some trawls traversed a diversity of habitats.

The spatial resolution of the trawling is an important factor in determining species distributions and habitat associations (Auster *et al.* 2001). In this study each trawl sampled an area of approximately 1000 m^2, which could only detect differences between seagrass (Group A) and unvegetated soft bottom (Group B). More directed trawling, targeting particular habitats (e.g. *Pinna bicolor* beds, *Posidonia* sp., *Malleus meridianus* beds etc) at a finer scale

(e.g. 2 minute trawls) would have the potential to demonstrate more detailed structure, especially for sub-dividing the Group B assemblage. This would require finer scale resolution of habitat types and their distribution throughout northern Spencer Gulf than is currently available although improved mapping is currently under way.

7.4.2 0+ snapper associations

The year 2006 had the highest abundances of 0+ snapper recorded over nine years in Spencer Gulf (Chapters IV and V). In spite of this, 0+ snapper were never found with the Group A assemblage which was characterised by strongly seagrass-associated species. This provides a strong indication that 0+ snapper do not utilise this habitat, even in exceptionally strong years. Thus, the extensive seagrass meadows in northern Spencer Gulf (Bryars 2003; Edyvane 2000), particularly on the eastern side, are a considerable area that is not suitable as a nursery for 0+ snapper. This may account for the distribution of 0+ snapper to the western side of the gulf, where seagrass meadows are less dominant (Chapter III). These results suggest that estimates of snapper density in northern Spencer Gulf can be refined and trawls that contain high abundances of *Siphonognathus radiatus* and *Stigmatopora argus* could be excluded from the area surveyed for 0+ snapper. If meadows of *Posidonia* spp. are excluded, the search area for other 0+ snapper nursery areas in South Australia is considerably reduced.

Age structure information indicates that strong year-classes have occurred once or twice per decade (Fowler *et al.* 2007) and the 2006 surveys produced high catches of 0+ snapper (Chapter IV). However, in that year, less than 60% of trawls classified as Group B contained snapper. The beam trawling, and the otter trawling that was done in conjunction with this study, indicated that in trawls where 0+ snapper were captured, their density was also higher in 2006 than in other years (Chapter IV). This indicates that other physical or biological factors exist that limit the distribution and abundance of 0+ snapper more so than the Group B assemblage with which they were associated.

Not all habitats in northern Spencer Gulf were sampled in this study. Trawling has been necessarily restricted to relatively flat bottom and away from rocky reefs. Whilst reef habitat is unusual in northern Spencer Gulf (Bryars 2003), there is an area of rocky reef near Point Lowly that is most notable as an aggregation point for cuttlefish, *Sepia apama*, during their reproductive season (Hall *et al.* 2007). This habitat could not be sampled in this study but is worthy of consideration as a nursery area for 0+ snapper especially in light of evidence in New Zealand where 0+ snapper utilise reef, albeit at lower densities than mud bottom (Kingett and Choat 1981).

The association between 0+ snapper and the Group B assemblage, which is defined by a suite of species that prefer bare soft bottom, is a result that is consistent with studies from Japan and New Zealand (Tanaka 1985; Francis 1995). 0+ snapper are most often associated with flat bare habitat, however, juvenile snapper can utilise more complex habitats. They have been found to use rocky reef in New Zealand (Kingett and Choat 1981; Thrush *et al.* 2002) and shallow *Zostera* beds in Japan and Victoria (Sudo *et al.* 1987; Hamer and Jenkins 2004). Furthermore, in Japan, *Zostera* beds were considered an important refuge from predation for juvenile snapper from piscivorous fish (Shoji *et al.* 2007). In Japan, habitat complexity is considered important for juvenile snapper to avoid predation (Shoji *et al.* 2007), but this does not appear to be the case for 0+ snapper in northern Spencer Gulf. The distribution of juvenile snapper in some regions is considered to be a function of food availability rather than habitat complexity (Azeta *et al.* 1980a; Sudo *et al.* 1983). It is possible, however, that foraging is less successful in the more complex habitat and that this may provide an explanation for the absence of 0+ fish in seagrass areas.

The use of specific fish species and assemblage distributions may have some value for identifying 0+ nursery areas in northern Spencer Gulf and identifying habitat associations. Current habitat mapping for this region does not distinguish any more habitats than those identified in this trawl survey by relating species and abundances to known habitat associations from the literature. Thus, the distinction between habitats could be made on the basis of the trawl assemblages identified in this study. Finally, 0+ snapper were not associated with the Group A assemblage even during strong recruitment years and this suggests that places with this assemblage can reasonably be excluded as potential nurseries for the species in northern Spencer Gulf.

Chapter VIII

General Discussion

8.1 Rationalisation

The number and strength of age classes available to South Australia's snapper fishery drives variation in catch over time, which is related to the population dynamics of the species (Fowler *et al.* 2007). This is driven by inter-annual variation in the recruitment of juveniles, i.e. 0+ fish (Fowler and Jennings 2003). Such variation is characteristic for many fish species and attempts that have been made to elucidate the sources of this variability have been the focus of considerable research effort (Rothschild 1986; Houde 1987; Fogarty *et al.*1991; Sinclair 1997; Rothschild 2000; Myers 2002). The aim of this thesis was to develop the understanding of the recruitment dynamics of snapper, *Chrysophrys auratus*, in order to facilitate the management of the fishery. This was done through a study of the reproductive biology of the adult fish and the biology and ecology of 0+ recruits in northern Spencer Gulf, South Australia. This small region has historically contributed greater than 50% of South Australia's commercial catch of snapper (Fowler *et al.* 2007). It supports large spawning aggregations of adult fish and it also has the only known nursery areas for 0+ snapper in South Australia (Fowler and Jennings 2003; Fowler *et al.* 2005b).

The annual trawl sampling done in this study provided compelling results on the annual patterns in the distribution and abundance of 0+ snapper. The spatial dispersion of 0+ recruits was consistent across years even though dramatic inter-annual variation in abundance of over 200 times occurred. These two observations provided the framework for the research described in this thesis.

8.2 Spatial patterns of recruitment

The distribution of 0+ snapper in northern Spencer Gulf was clumped at two spatial scales. The trawl sampling was done in the northern half of Spencer Gulf and 0+ snapper were only found in the northern reaches of this region, particularly on the western side of the gulf. In this zone, 0+ snapper were found regularly in only four small areas. This pattern of

dispersion was consistent between years. Furthermore, one of the areas, Western Shoal, also consistently had higher abundances of 0+ snapper than the other areas. These patterns were also consistent with earlier work (Fowler and Jennings 2003). The results indicate the involvement of processes that determine the distribution patterns of 0+ snapper which act independently of recruitment strength. It is also likely that different environmental processes are responsible for the regional and local patterns of distribution.

At the regional scale, the pattern of distribution may be influenced by the proximity to the spawning grounds and the processes of advection of larvae (Beck *et al.* 2001; Juanes 2007). In the study region, the northerly trend in the distribution of 0+ recruits may have resulted from larval supply related to currents or prevailing wind conditions. This is consistent with the predominance of south-easterly winds in South Australia during summer which may set up currents that deliver larvae to the north-west. Futhermore, a large spawning aggregation is known to form every year at a location that is to the south-west of the major nursery area, near Western Shoal.

The smaller scale distribution pattern may result from habitat selectivity and mortality during the transition and early post-settlement phases (Juanes 2007). Two factors i.e. habitat and food that may influence distribution of recruits were considered in this study. Previous research indicated that the pattern of dispersion was correlated with the distribution of fine sediment substratum (Fowler and Jennings 2003). Habitat mapping in northern Spencer Gulf indicates that those areas where 0+ snapper were captured were characterised as unvegetated soft bottom whilst much of the area where no 0+ snapper were captured supported seagrass meadows (Edyvane 2000; Bryars 2003). This observation was confirmed in this study by the dissociation between 0+ snapper and the assemblage of fish and macroinvertebrates that were associated with seagrass. Nevertheless, large parts of northern Spencer Gulf with apparently suitable habitat i.e. unvegetated soft bottom, did not support 0+ snapper.

The pattern of distribution may also result from food availability as hypothesised for snapper in Japan and New Zealand, (Azeta *et al.* 1980a; Sudo *et al.* 1983; Francis 1997). However, dietary analysis of 0+ snapper from northern Spencer Gulf indicated that even early post-settlement snapper are generalist feeders, taking a wide array of taxa. Consequently, this is unlikely to be a major factor affecting the distribution pattern. The habitats that 0+ snapper occurred in were not complex and are unlikely to provide substantial protection from predators. That 0+ snapper did not occur in the more complex habitat in northern Spencer Gulf suggests that that predation may be less important in shaping the pattern of dispersion there than elsewhere in their range. Habitat selectivity may account for some of the pattern as

larvae of snapper have exhibited some selectivity at small scales during their settlement phase in estuaries in eastern Australia (Trnski 2002). Such selectivity may be for low-energy environments, especially as 0+ snapper are found in greater abundance in fine-sediment areas.

In this study, key areas for recruitment of 0+ snapper in northern Spencer Gulf, which are important for the dynamics of South Australia's snapper population, were identified. A framework for the identification of other possible nursery areas and for the assessment of their value in terms of food resources was also provided. The opportunity to focus future studies of recruitment on particular areas and habitat types now exists. It is likely that the regional pattern of dispersion results from physical processes that deliver larvae to the north and that the local pattern is the result of selection of suitable areas by larvae or early post-settlement juveniles. The suitability of these areas is at least partly the result of food availability and habitat type. However, why the vast and productive seagrass beds of northern Spencer Gulf are not utilised by 0+ snapper is not known. To further the understanding of the distribution patterns of snapper recruits in northern Spencer Gulf the distribution and behaviour of snapper during the late larval phase requires study.

8.3 Inter-annual recruitment variation

Trawl sampling in northern Spencer Gulf over the past nine years has indicated that recruitment of 0+ snapper varies dramatically, up to 200 times. In some years, almost no recruitment occurred but in one year in particular, i.e. 2006, large numbers of 0+ recruits were captured. Such variation in recruitment of 0+ fish can result from environmentally-mediated impacts on egg production, egg and larval survival, early post settlement survival or a combination of these.

8.3.1 Egg production

The impact of egg production on recruitment strength was considered. This required a detailed understanding of the reproductive dynamics of the species (Marshall *et al.* 1998; Witthames and Marshall 2008). The research confirmed that snapper is a multiple batch spawning species, capable of spawning over consecutive days. Furthermore, the study documented the intra-seasonal pattern in egg production. Histological examination of ovaries of mature females indicated that spawning began in late November, at a time when water temperature was between 18ºC and 20ºC, and continued until late January or early February during times when water temperature exceeded 24ºC. Nevertheless, a major finding was that egg production varied through the spawning season and that the peak in egg production occurred in December each year when the majority of fish were on the spawning grounds and

individual fish were spawning thousands to hundreds of thousands of eggs on a daily basis. Importantly, the pattern of egg production did not vary between the first two seasons studied but in 2007/08, the spawning season was considerably shorter, the interval between spawning events was longer but the number of eggs spawned in each event was higher. These inter-annual patterns in egg production were compared to the recruitment rates of snapper in these years. The first season produced the strongest recruitment ever observed whereas the second season resulted in recruitment of approximately 1/3rd the magnitude, despite almost identical patterns of spawning. The pattern of egg production differed in the last season but a large amount of egg production still occurred which nevertheless resulted in almost no recruitment. These data suggested that it was unlikely that differences in egg production between years accounted for the observed differences in recruitment rates. As such, focus was directed to the early life history processes.

8.3.2 Mortality in the early life history

The environmental influence on the life history was considered through analysis of the microstructure of the otoliths of 0+ snapper collected in the trawls. The data were interpreted to provide spawn dates, settlement dates, pre-settlement duration and growth rate for individual fish. These data were then compared with the environmental characteristics, i.e. temperature, lunar phase, tidal magnitude, to determine those conditions that led to successful development and recruitment.

Pre-settlement duration and growth rate

Growth rate is an important influence on the success of fish recruitment (Houde 1987). For snapper, water temperature has been linked to growth rates and short larval duration in New Zealand (Francis 1994b), and was thought to influence recruitment rates (Francis 1993; Francis *et al.* 1997). Earlier work in northern Spencer Gulf indicated that shorter pre-settlement durations were associated with stronger recruitment years (Fowler and Jennings 2003). In the recent work 0+ recruits with short pre-settlement durations were again present in the strong recruitment year of 2006 and not in the weaker recruitment years. However, no relationship between short larval duration and warmer water was detected. Furthermore, in northern Spencer Gulf, growth rate of 0+ snapper did not appear to be affected by water temperature through the pre-settlement period. Thus, the impact of water temperature on growth rate and pre-settlement duration appears not to explain the variation in recruitment. This suggests that, in some weak recruitment years, environmental variables other than temperature can limit the speed of development from spawning to settlement competency.

The lack of a relationship between growth rate and temperature observed in this study is unusual for pre-settlement fish (Houde 1989). The water temperatures recorded for the study region for December, January and February, i.e. through the period the larvae were developing, were at the upper limit of those observed for the species elsewhere (Francis 1994b), and even higher than those used to grow out snapper in aquaculture (Foscarini 1988). Thus, it is likely that the successful recruits considered in this study were exposed to water temperatures during their larval life that allowed them to grow at or near their maximum rate. However, pre-settlement duration did vary by up to ten days indicating other influences also affect pre-settlement duration. Aquaculture research has identified that the availability of food and salinity are both important in controlling pre-settlement growth (Fielder *et al.* 2005). Currently, the data available on the physical and biological properties of northern Spencer Gulf are not detailed enough to test hypotheses that relate growth and recruitment to such factors. However, salinity in parts of Spencer Gulf can reach levels of over 45‰ (Nunes and Lennon 1986), which is sufficient to retard the growth and development of larvae (Fielder *et al.* 2005).

Spawning and survivorship

The most significant contribution of this work is the comparison between the estimated temporal pattern in egg production and the timing of successful spawning, as estimated from spawn dates of 0+ recruits and the corresponding water temperature and lunar conditions.

Considerable intra-annual variation in the frequency distributions of spawn dates occurred. There were disjunct periods from which recruits originated and the number of recruits that originated from these periods varied dramatically. There was also inter-annual variation in the timing of the origin and magnitude of recruitment. In contrast to this, the peak in egg production was inter-annually stable (December) and considerable spawning occurred during December and into January of each year but recruitment did not always result. Thus, inter-annual recruitment variation was not controlled by reproductive output and the relationship between egg production and recruitment was obscured by pre-recruitment mortality. There was also no evidence that the intra-annual pattern of recruitment resulted from variation in egg production as spawning output was high throughout the period, but subtle weekly or daily variations in egg production could not be detected.

In contrast to the variation in the timing of origin of recruits, there were some consistent patterns in the environmental conditions that led to successful recruitment. Peaks in spawning success were correlated with the lunar cycle in two years of sampling, specifically on lunar quarters. This effect may result from subtle variation in egg production or larval

transport and/or mortality processes at either spawning or settlement. The former is unlikely as numbers of actively spawning fish were sampled on all lunar phases. Around the lunar quarters, tidal flows are weakest and light conditions are also not extreme and this may have an effect on predation rates or larval delivery to the nursery areas. A final possibility to explain the pattern is that fertilisation rates are higher during weaker tidal flows.

Water temperature had a consistent impact on the recruitment processes. It was clear that spawning occurred at a lower temperature than that which gave rise to successful recruits. Thus, water temperature had a strong effect on egg survival. By far the majority of successful recruits were spawned when water temperature conditions exceeded 21ºC. There is evidence for snapper elsewhere that water temperature is an important part of the recruitment processes (Francis 1994b; Francis *et al.* 1997), as it is for many other species (Houde 1987). However, the water temperature required for successful spawning in snapper appears to be higher in northern Spencer Gulf than for elsewhere.

These results are compelling and offer some explanation for the variations in recruitment but are insufficient to explain the magnitude of the variation. This is most apparent when the failure of recruitment in 2008 is considered. In that year, suitable water temperatures at spawning and for development and growth were present for much of December and January and were coincident with four lunar quarters, but no recruits eventuated from these spawning periods. In the other years too, suitable conditions occurred for considerable periods of the spawning seasons but recruitment did not always result. Thus, whilst water temperature can have an impact on recruitment processes, particularly below 21ºC, other environmental variation must also have an impact on mortality in the early life history to result in the magnitude and timing of recruitment observed in this study. There are a multitude of possibilities that result in mortality in the early life stages including starvation, predation or physical damage through environmental extremes such as storm events.

8.4 Future research

This study on the reproductive biology and recruitment dynamics of snapper in northern Spencer Gulf has provided information on the spawning dynamics, distribution and abundance of 0+ juveniles and the environmental impacts on recruitment. Several potential lines of further inquiry have emerged from the research.

8.4.1 Is egg production affected by lunar periodicity?

Peaks in recruitment occurred from spawning on the lunar quarters (Chapter V). This pattern was most likely set either as a result of changes in spawning or mortality at settlement. This was not addressed in this study because the present reproductive data set was insufficient to test the observation. It was clear that spawning occurred during all lunar phases but the intensity of this may have varied more subtly, i.e. through variation in batch fecundity or spawning frequency. To test this, would require daily sampling of large numbers of adult females on all lunar phases with sufficient intensity to accurately determine egg production. Alternatively, egg abundances in the plankton could be measured at a suitably fine temporal scale.

8.4.2 What controls the distribution of 0+ recruits?

The spatial dispersion of recruits was extremely stable across multiple years. The successfully spawned 0+ recruits were generalist feeders but were associated with a particular species assemblage. The stable distribution must result from inter-annually constant influences on 0+ snapper, but whether these patterns are set at settlement or result from larval distribution patterns remains unknown. Given the broad habitat use by snapper in other parts of the world, the latter is more likely. This hypothesis could be tested with a study of larval distributions in the gulf throughout the reproductive and recruitment periods.

8.4.3 When is 0+ recruitment strength set?

This study has demonstrated that 0+ snapper recruitment strength is set in the early life history but is not related to variation in egg production, suggesting that recruitment strength is the result of mortality between spawning and the time of 0+ sampling. Direct assessment of egg and larval abundances may yield answers, but this would involve intensive plankton sampling throughout December and January. The agents of mortality, such as starvation and predation, also need to be considered closely. Significant progress toward understanding the processes of recruitment could be gained if the timing of failure of a year-class was determined, i.e. does recruitment failure occur at the egg stage, early larval stage or during the transition phase?

These three lines of inquiry can all be addressed through plankton sampling. However, such sampling would need to be done several times a week, which is a temporal scale that may be prohibitively expensive. This research strategy would provide the opportunity to overcome one of the major difficulties with the research done in this study, namely, that information on the biology of unsuccessful recruits could not be collected. The direct study of the processes of mortality during the planktonic phase is the next important step in our understanding of the recruitment dynamics of snapper in northern Spencer Gulf.

References

Adams, A. J., Dahlgren, C. P., Kellison, G. T., Kendall, M. S., Layman, C. A., Ley, J. A., Nagelkerken, I., and Serafy, J. E. (2006). Nursery function of tropical back-reef systems. *Marine Ecology Progress Series* **318**, 287-301.

Alheit, J. (1993). Use of the daily egg production method for estimating biomass of clupeoid fishes: a review and evaluation. *Bulletin of Marine Science* **53**, 750-767.

Allman, R. J., and Grimes, C. B. (2002). Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructure. *Fishery Bulletin* **100**, 391-403.

Anderson, C. S. (1995). Calculating size-dependent relative survival from samples taken before and after selection. In 'Recent developments in fish otolith research'. (D. H. Secor, J. M. Dean and S. E. Campana). pp. 455–466. (University of South Carolina Press: Columbia, USA.)

Auster, P. J., Joy, K., and Valentine, P. C. (2001). Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example (Northwest Atlantic, Gulf of Maine). *Environmental Biology of Fishes* **60**, 331-346.

Australian Hydrographic Services (2006). 'Point Riley to Port Augusta. Chart Number Aus 778.' (Australian Hydrographic Services: New South Wales, Australia.)

Azeta, M., Ikemoto, R., and Azuma, M. (1980a). Distribution and growth of demersal 0-age red sea bream, *Pagrus major*, in Shijiki Bay. *Bulletin of the Seikai Regional Fisheries Research Laboratory* **54**, 259-277.

Azeta, M., Ikemoto, R. and Azuma, M. (1980b). Diurnal activity rhythms in 0-group red sea bream *Pagrus major*. *Bulletin of the Seikai Regional Fisheries Laboratory* **54**, 279-289.

Bagenal, T. B. (1973). Fish fecundity and its relations with stock and recruitment. *Rapport et Procès-verbaux des Réunions Conseil Permanent International pour l'Exploration de la Mer* **164**, 186-198.

Bailey, K. M., and Houde, E. D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances In Marine Biology* **25**, 1-83.

Bakun, A. (1996). 'Patterns in the Ocean: Ocean Processes and Marine Population Dynamics.' (University of California Sea Grant: San Diego, California, USA.)

Bastow, T. P., Jackson, G., and Edmonds, J. S. (2002). Elevated salinity and isotopic composition of fish otolith carbonate: stock delineation of pink snapper, *Pagrus auratus*, in Shark Bay, Western Australia. *Marine Biology* **141**, 801-806.

Bauman, H., Hinrichsen, H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L. W., and Temming, A. (2006). Linking growth to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling. *Fisheries Oceanography* **15**, 465-476.

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., and Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**, 633-641.

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., and Weinstein, M. P. (2003). The role of nearshore ecosystems as fish and shellfish nurseries. *Issues in Ecology* **11**, 1-12.

Beverton, R. J. H. (1962). Long-term dynamics of certain North Sea fish populations. In 'The Exploitation of Natural Animal Populations' (Eds E. D. Le Cren and M. W. Holdgate.) pp. 242-264. (Blackwell Publishing: London, UK.)

Beyer, J. E. (1989). Recruitment stability and survival - simple size-specific theory with examples from the early life dynamics of marine fish. *Dana* **7**, 45–147.

Bradford, M. J. (1992). Precision of recruitment predictions from early life stages of marine fishes. *Fishery Bulletin* **90**, 439-453.

Bradford, M. J., and Cabana, G. (1995). Interannual variability in survival rates and the causes of recruitment variability. In 'Early life history and recruitment in fish populations' (Eds R. C. Chambers and E. A. Hall.) pp. 469-494. (Chapman and Hall: London, UK.)

Bryars, S. (2003). 'An Inventory of Important Coastal Fisheries Habitats in South Australia. Fish Habitat Program.' (Primary Industries and Resources: Adelaide, Australia.)

Bye, J. A. T. (1984). Exchange processes for upper Spencer Gulf, South Australia. *Transactions of the Royal Society of South Australia* **105**, 60-66.

Bureau of Meteorology (2008). Bureau of Meteorology Website. www.bom.gov.au [accessed on 10th December 2008].

Campana, S. E. (1996). Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* **135**, 21-26.

Campana, S. E., and Jones, C. M. (1992). Analysis of otolith microstructure data. In 'Otolith microstructure examination and analysis'. Canadian Special Publications Fisheries and Aquatic Sciences No 117. (Eds D.K. Stevenson and S.E. Campana.) pp. 73-100. (Canadian Department of Fisheries and Oceans: Ottawa, Canada.)

Cargnelli, L. M., and Gross, M. R. (1996). The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 360-367.

Carrick, N. A. (2003). 'Spencer Gulf Prawn (*Melicertus latisulcatus*) Fishery. Fishery Assessment report to PIRSA.' SARDI Aquatic Sciences Publication No RD03/0079-2. (South Australian Research and Development Institute: Adelaide, Australia.)

Casper, R. M., Jarman, S. N., Gales, N. J., and Hindell, M. A. (2007). Combining DNA and morphological analyses of faecal samples improves insight into trophic interactions: a case study using a generalist predator. *Marine Biology* **152**, 815-825.

Castriota, L., Finoia, M. G., Campagnuolo, S., Pipitone, C., and Andaloro, F. (2006). Diet of juvenile *Pagrus pagrus* (Sparidae) from sandy bottoms of the southern Tyrrhenian Sea. *Cybium* **30**, 291-295.

Chambers, R. C., and Leggett, W. C. (1987). Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1936-1947.

Chatfield, C. (1996). 'The Analysis of Time Series: An Introduction.' (Chapman and Hall, London.)

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143.

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in intertidal communitites. *Journal of Experimental Marine Biology and Ecology* 93, 11-45.

Coutin, P. C. (1997). 'Snapper – 1996. Fisheries Victoria Assessment Report No.12' (Marine and Freshwater Resources Institute: Victoria, Australia.)

Coutin, P. C., Cashmore, S., and Sivakumuran, K. P. (2003). 'Assessment of the snapper fishery in Victoria.' Final Report to FRDC for project No. 97/128. (Fisheries Research and Development Corporation: Canberra, Australia.)

Crossland, J. (1977a). Fecundity of the snapper *Chrysophrys auratus* (Pisces: Sparidae) from the Hauraki Gulf. *New Zealand Journal of Marine and Freshwater Research* **11**, 767-775.

Crossland, J. (1977b). Seasonal reproductive cycle of snapper *Chrysophrys auratus* (Forster) in the Hauraki Gulf. New *Zealand Journal of Marine and Freshwater Research* **11**, 37-60.

Cushing, D. H. (1975). 'Marine Ecology and Fisheries'. (Cambridge University Press: Cambridge, UK.)

Cushing, D. H. (1981). 'Fisheries Biology. A study in Population Dynamics.' 2nd Edn. (The University of Wisconsin Press: Wisconsin, USA.)

Cushing, D. H. (1988). The study of stock and recruitment. In 'Fish Population Dynamics' (Ed. J. A. Gulland) pp. 105-128. (Wiley: Chinchester, UK.)

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances In Marine Biology* **26**, 249-293.

Cushing, D. H. (1996). 'Towards a Science of Recruitment in Fish Populations.' (Ecology Institute: Oldendorf-Luhe, Germany.)

Cushing, D. H., and Horwood. J.W. (1994). The growth and death of fish larvae. *Journal of Plankton Research* **16**, 291-300.

Danilowicz, B. S., and P. F. Sale. (1999). Relative intensity of predation on the French grunt, *Haemulon flavolineatum*, during diurnal, dusk, and nocturnal periods on a coral reef. *Marine Biology* **133**, 337-343.

Davies, N. M., and Walsh, C. (1995). Length and age composition of commercial snapper landings in Auckland Fishery Management Area, 1988-94. New Zealand Fisheries Data Report No. 58. (Ministry of Fisheries: Wellington, New Zealand.

DeMartini, E. E. (1991). Annual variations in fecundity, egg size, and the gonadal and somatic conditions of queenfish *Seriphus politus* (Sciaenidae). *Fishery Bulletin* **89**, 9-18.

Derbal, F., Nouacer, S., Kara, M. H. (2007). Diet of the annular seabream *Diplodus annularis* (Sparidae) of the Gulf of Annaba (eastern Algeria). *Cybium* **31**, 443-450.

Doherty, P. J. (2002). Variable replenishment and the dynamics of reef fish populations, In 'Coral Reef Fishes dynamics and diversity in a complex ecosystem' (Ed. P. F. Sale) pp. 327-355. (Academic Press: California, USA.)

Doherty, P., and Fowler, A. J. (1994). An empirical test of recruitment limitation in a coral reef fish. *Science* **263**, 935-939.

Doherty, P., and Williams, D. M. (1988). The replenishment of coral reef fish populations. *Annual Review of Oceanography and Marine Biology* **26**, 487-551.

Edgar, G. J., and Shaw, C. (1995). The production and trophic ecology of shallow-water fish assemblages in southern Australia I. Species richness, size-structure and production of fishes in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* **194**, 53-81.

Edmonds, J. S., Moran, M. J., and Caputi, N. (1989). Trace element analysis of fish sagittae as an aid to stock identification: pink snapper (*Chrysophrys auratus*) in Western Australian waters. *Canadian Journal of Fisheries and Aquatic Science* **46**, 50–54.

Edyvane, K. S. (2000). Conserving marine biodiversity in South Australia. Part 2 - Identification of areas of high conservation value in South Australia. SARDI Research Report Series no. 39. (South Australian Research and Development Institute: Adelaide, Australia.)

Edyvane, K. S., and Baker, J. L.. (1996). Marine Biogeography of Spencer Gulf, South Australia. Final Report to the Australian Nature Conservation Agency. (South Australian Research and Development Institute: Adelaide, Australia.)

Ferrell, D. J., and Sumpton, W. (1998). 'Assessment of the fishery for snapper (*Pagrus auratus*) in Queensland and New South Wales.' Final Report to the FRDC for project no. 93/074. (Fisheries Research and Development Corporation: Canberra, Australia.)

Fielder, D. S., Bardsley, W. J., Allan, G. L., and Pankhurst, P. M. (2005). The effects of salinity and temperature on growth and survival of Australian snapper, *Pagrus auratus* larvae. *Aquaculture* **250**, 201-214.

Findlay, A. M., and Allen, L. G. (2002). Temporal patterns of settlement in the temperate reef fish *Paralabrax clathratus*. *Marine Ecology Progress Series* **238**, 237-248.

Flinders Ports (2008). 2008 Tide Book for South Australian Ports. (South Australian Government: South Australia, Australia.)

Fogarty, M. J., Sissenwine, M. P., and Cohen, E. B. (1991). Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution* **6**, 241-246.

Fogarty, M. J., Myers, R. A., and Bowen, K. G. (2001). Recruitment of cod and haddock in the North Atlantic: a comparative analysis. *ICES Journal of Marine Science* **58**, 952-961.

Foscarini, R. (1988). A review: Intensive farming procedures for red sea bream (*Pagrus major*) in Japan. *Aquaculture* **72**, 191-246.

Fowler, A. J., and Jennings, P. R. (2003). Dynamics in 0+ recruitment and early life history for snapper (*Pagrus auratus*, Sparidae) in South Australia. *Marine and Freshwater Research* **54**, 941-956.

Fowler, A. J., Gillanders, B. M., and Hall, K. C. (2004). 'Adult migration, population replenishment and geographic structure for snapper in SA.' Final Report to FRDC for project No. 2002/001. (Fisheries Research and Development Corporation: Canberra, Australia.)

Fowler, A. J., McGarvey, R., Feenstra, J. E., Jackson, W. B., and Jennings, P. R. (2005a). 'Snapper (*Pagrus auratus*) Fishery. Fishery Assessment Report to PIRSA for the Marine Scalefish Management Committee.' SARDI Aquatic Sciences Publication No RD03/0068-2. (South Australian Research and Development Institute: Adelaide, Australia.)

Fowler, A. J. Gillanders, B. M., and Hall, K. C. (2005b). Relationship between elemental concentration and age from otoliths of adult snapper (*Pagrus auratus*, Sparidae): implications for movement and stock structure. *Marine and Freshwater Research* **56**, 661-676.

Fowler, A. J., McGarvey, J. E., Feenstra, J. E., and Jackson, W. B. (2007). 'Snapper (*Pagrus auratus*) Fishery.' SARDI Aquatic Sciences Publication No. F2007/00523-1. (South Australian Research and Development Institute: Adelaide, Australia.)

Fox, C. J., Geffen, A. J., Taylor, N., Davison, P., Rossetti, H., and Nash, R. D. M. (2007). Birth-date selection in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea (British Isles). *Marine Ecology Progress Series* **345**, 255-269.

Francis, M. P. (1993). Does water temperature determine year-class strength in New Zealand snapper (*Pagrus auratus*, Sparidae)? *Fisheries Oceanography* **2**, 65-72.

Francis, M. P. (1994a). Duration of larval and spawning periods in *Pagrus auratus* (Sparidae) determined from otolith daily increments. *Environmental Biology of Fishes* **39**, 137-152.

Francis, M. P. (1994b). Growth of juvenile snapper, *Pagrus auratus*. New *Zealand Journal of Marine and Freshwater Research* **28**, 201-218.

Francis, M. P. (1995). Spatial and seasonal variation in the abundance of juvenile snapper (*Pagrus auratus*) in the north-western Hauraki Gulf. *New Zealand Journal of Marine and Freshwater Research* **29**, 565-579.

Francis, M. P. (1997). Condition cycles in *Pagrus auratus*. *Journal of Fish Biology* **51**, 583-600.

Francis, M. P., Paul, L. J., and Mulligan, K. P. (1992). Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection. *Australian Journal of Marine and Freshwater Research* **43**, 1069-1089.

Francis, M. P., Langley, A. D., and Gilbert, D. J. (1997). Prediction of snapper (*Pagrus auratus*) recruitment from sea surface temperature. In '2nd World Fisheries Congress. Developing and sustaining world fisheries resources: The state of science and management.' (Eds D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer.) pp. 67-71. (CSIRO Publishing: Victoria, Australia.)

Francis, R. I. C. C. (2006). Measuring the strength of environment-recruitment relationships: the importance of including predictor screening within cross-validation. *ICES Journal of Marine Science* **63**, 594-599.

Froese, R., and Pauly, D. (Eds) (2008). FishBase. Available at www.fishbase.org, version (12/2008).

Fukuhara, O. (1985). Functional morphology and behaviour of early life stages of red sea bream. *Bulletin of the Japanese Society of Scientific Fisheries* **51**, 731-743.

Furlani, D., Gales, R., and Pemberton, D. (2007). 'Otoliths of Common Australian Temperate Fish. A Photographic Guide.' (CSIRO Publishing, Victoria, Australia.)

Gilbert, D. J. (1997). Towards a new recruitment paradigm for fish stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 969-977.

Gillanders, B. M., and Kingsford, M. J. (1996). Influence of habitat on abundance and size structure of a large temperate-reef fish, *Achoerodus viridis* (Pisces: Labridae). *Marine Biology* **132**, 503-514.

Gillanders, B. M., Able, K. W., Brown, J. A., Eggleston, D. B., and Sheridan, P. F. (2003). Evidence for connectivity between juvenile & adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series* **247**, 281-295.

Gisbert, E., Conklin, D. B., and Piedrahita, R. H. (2004). Effects of delayed first feeding on the nutritional condition and mortality of California halibut larvae. *Journal of Fish Biology* **64**, 116-132.

Gladstone, W. (2007). Temporal patterns of spawning and hatching in a spawning aggregation of the temperate reef fish *Chromis hypsilepis* (Pomacentridae). *Marine Biology* **151**, 1143-1152.

Godfriaux, B. L. (1969). Food of predatory demersal fish in the Hauraki Gulf. *New Zealand Journal of Marine and Freshwater Research* **3**, 518-544.

Godfriaux, B. L. (1974). Food of snapper in the western Bay of Plenty, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **8**, 473-504.

Gomon, M. F., Bray, D., and Kuiter, R. (2008). 'Fishes of Australia's Southern Coast.' (New Holland Publishers: Sydney, Australia.)

Gowlett-Holmes, K. (2008). 'A Field Guide to the Marine Invertebrates of South Australia.' (Notomares: Tasmania, Australia.)

Hall, K.C. (2002). The Life History and Fishery of *Sepia apama*. Ph.D. Thesis, University of Adelaide, Adelaide, South Australia.

Hall, K. C., Fowler, A. J. and Geddes, M. C. (2007). Evidence for multiple year-classes of the giant Australian cuttlefish *Sepia apama* in northern Spencer Gulf, South Australia. *Reviews in Fish Biology and Fisheries* **17**, 367-384.

Hamer, P. A., and Jenkins, G. P. (2004). High levels of spatial and temporal recruitment variability in the temperate sparid *Pagrus auratus*. *Marine and Freshwater Research* **55**, 663-673.

Hamer, P. A., Jenkins, G. P., and Welsford, D. (1998). 'Sampling of Newly-settled Snapper¸ *Pagrus auratus*, and Identification of Preferred Habitats in Port Phillip Bay – A Pilot Study.' Marine and Freshwater Resources Institute, Queenscliff, Victoria. Project No 96/297. (Fisheries Research and Development Corporation: Canberra, Australia.)

Hardman, W. H., and Southward, G. M. (1957). Investigations of small halibut in September 1955. IPHC Report 25, 22-27. (International Pacific Halibut Commission: Seattle, USA.)

Higuchi, M. (1977). Mariculture in warm seas: present status of mariculture in the Seto Inland Sea. In 'Proceedings of the Thirds Japan-Soviet Symposium on Aquaculture.' (Ed. S. Motoda) pp. 157-171. (Tokai University: Tokyo, Japan)

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe. *Rapports et Procès - verbaux des Réunions, Conseil Permanent International pour l'Exploration de la Mer* **20**, 1-228.

Hjort, J. (1926). Fluctuations in the year-classes of important food fishes. *Journal du Conseil* **1**, 1-38.

Holladay, B. A., and Norcross, B. L. (1995). August diet of age-0 Pacific halibut in nearshore waters of Kodiak Island, Alaska *Environmental Biology of Fishes* **44**: 403-416.

Horn, P. L. (1986). Distribution and growth of snapper *Chrysophrys auratus* in the North Taranaki Bight, and management implications of these data. New Zealand *Journal of Marine and Freshwater Research* **20**, 419-430.

Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium* **2**, 17-29.

Houde, E. D. (1989). Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin* **87**, 471-495.

Hunter, J. R., and Macewicz, B. J. (1985). Measurement of spawning frequency in multiple spawning fishes. In 'An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*.'(Ed. R. Lasker.) pp. 79-94. US National Marine Fisheries Service, National Oceanic and Atmospheric Administration Technical Report 36, La Jolla, California.

Hunter, J. R., Lo, N. C. H., and Roderick, J. H. L. (1985). Batch fecundity in multiple spawning fishes. In 'An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*.'(Ed. R. Lasker.) pp. 67-78. US National Marine Fisheries Service, National Oceanic and Atmospheric Administration Technical Report 36, La Jolla, California.

Huston, M. A. (1999). Local processes and regional patterns: appropriate scales for understanding variation in plants and animals. *Oikos* **86**, 393-401.

Hutchings, P. A., Ward, T. J., Waterhouse, J. H., and Walker, L. (1993). Infauna of marine sediments and seagrass beds of upper Spencer Gulf near Port Pirie, South Australia. *Transactions of the Royal Society of South Australia* **117**, 1-15.

Jackson, G., and Cheng, Y. W. (2001). Parameter estimation with egg production surveys to estimate snapper, *Pagrus auratus*, biomass in Shark Bay, Western Australia. *Journal of Agricultural Biological and Environmental Statistics* **6**, 243-257.

Jenkins, G. P., Wheatley, M. J., and Poore, A. G. B. (1996). Spatial variation in recruitment, growth, and feeding of postsettlement King George whiting, *Sillaginodes punctata*, associated with seagrass beds of Port Phillip Bay, Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 350-359.

Johnson, M. S., Creagh, S., and Moran, M. (1986). Genetic subdivision of stocks of snapper *Chrysophrys unicolor*, in Shark Bay, Western Australia. *Australian Journal of Marine and Freshwater Research* **37**, 337-345.

Jones, G. P. (1986). Food availability affects growth in a coral reef fish. *Oecologia* **70**, 136-139.

Juanes, F. (2007). Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. *Journal of Fish Biology* **70**, 661-677.

Kailola, P. J., Williams, M. J., Steward, P. C., Reichelt, R. F., McNee, A., and Grieve, C. (1993). 'Australian Fisheries Resources.' (Imprint Limited: Brisbane, Australia.)

Kaufman, L. J., Ebersole, J., Beets, J., and McIvor, C. C. (1992). A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Environmental Biology of Fishes* **34**, 109-118.

Kingett, P. D., and Choat, J. H. (1981). Analysis of density and distribution patterns in *Chrysophrys auratus* (Pisces: Sparidae) within a reef environment: an experimental approach. *Marine Ecology Progress Series* **5**, 283-290.

Kojima, K. (1981). Growth of the red sea bream (*Pagrus major*) in young stages in Yuya Bay, the Japan Sea. *Bulletin of the Seikai Regional Fisheries Research Laboratory* **56**, 55-70.

Kraus, R. T., and Secor, D. H. (2005). Application of the nursery-role hypothesis to an estuarine fish. *Marine Ecology Progress Series* **291**, 301–305.

Kurita, Y., Nemoto, Y., Oozeki, Y., Hayahizaki, K., and Ida, H. (2004). Variations in patterns of daily changes in otolith increment widths of 0+ Pacific saury, *Cololabis saira*, off Japan by hatch date in relation to the northward feeding migration during spring and summer. *Fisheries Oceanography* **13**, 54-62.

Langton, R. W., Steneck, R. S., Gotceitas, V., Juanes, F., and Lawton, P. (1996). The interface between fisheries research and habitat management. *North American Journal of Fisheries Management* **16**, 1-7.

Lapolla, A., and Buckley, L. J. (2005). Hatch date distributions of young-of-year haddock *Melanogrammus aeglefinus* in the Gulf of Maine/Georges Bank region: implications for recruitment. *Marine Ecology Progress Series* **290**, 239-249.

Lasker, R. (1975). Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. *Fisheries Bulletin of the United States Department of Commerce* **73**, 453-462.

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003). Settlement and distribution of age-0 juvenile cod, *Gadus morhua*, and *G. ogac*, following a large scale habitat manipulation. *Marine Ecology Progress Series* **262**, 241-252.

Levin, P. S. (1994). Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. *Environmental Biology of Fishes* **40**, 271-281.

Levin, P. S. (1996). Recruitment in a temperate demersal fish: Does larval supply matter? *Limnology and Oceanography* **41**, 672-679.

MacArthur, L. D., and Hyndes, G. A. (2001). Differential use of seagrass assemblages by a suite of odacid species. *Estuarine, Coastal and Shelf Science* **52**, 79-90.

Marshall, C. T., and Frank, K. T. (1999). The effect of interannual variation in growth and condition on haddock recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 347-355.

Marshall, C. T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P., and Ulltang, Ø. (1998). Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1766-1783.

Matsuyama, M., Matsuura, S., Ouchi, Y., and Hidaka, T. (1987). Maturity classification and group maturity of the red sea bream *Pagrus major*: I. Female maturity. *Marine Biology* **96**, 163-168.

Matsuyama, M., Adachi, S., Nagahama, Y., and Matsuura, S. (1988). Diurnal rhythm of oocyte development and plasma steroid hormone levels in the female red sea bream, *Pagrus major*, during the spawning season. *Aquaculture* **73**, 357-372.

Matsuyama, M., Nagahama, Y., and Matsuura, S. (1991). Observations on ovarian follicle ultrastructure in the marine teleost, *Pagrus major*, during vitellogenesis and oocyte maturation. *Aquaculture* **92**, 67-82.

McGlennon, D. (2003). The fisheries biology and population dynamics of snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. Ph.D. Thesis. University of Adelaide, Adelaide, South Australia.

McGlennon, D., and Jones, G. K. (1997). Snapper (*Pagrus auratus*), South Australian Fisheries Assessment Series 97/07. (South Australian Research and Development Institute: Adelaide, Australia.)

McGlennon, D., Jones, G. K., Baker, J., Jackson, W. B., and Kinloch, M. A. (2000). Ageing, catch-at-age and relative year-class strength for snapper (*Pagrus auratus*) in northern Spencer Gulf, South Australia. *Marine and Freshwater Research* **51**, 77-677.

Mertz, G., and Myers, R. A. (1994). The ecological impact of the Great Salinity Anomaly in the northern Northwest Atlantic. *Fisheries Oceanography* **3**, 1-14.

Mertz, G., and Myers, R. A. (1996). Influence of fecundity on recruitment variability of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 1618-1625.

Methot, R. D. (1983). Seasonal variation in the survival of larval northern anchovy, *Engraulis mordax*, estimated from age distributions of juveniles. *Fishery Bulletin* **81**, 741-750.

Mihelakakis, A., and Yoshimatsu, T. (1998). Effects of salinity and temperature on incubation period, hatching rate and morphogenesis of the red sea bream. *Aquaculture International* **6**, 171-177.

Moran, M., Burton, C., and Jenke, J. (2002). Sexual and local variation in head morphology of snapper, *Pagrus auratus*, Sparidae, in the Shark Bay region of Western Australia. *Marine and Freshwater Research* **50**, 27-34.

Moran, M., Burton, C., and Jenke, J. (2003). Long-term movement patterns of continental shelf and inner gulf snapper (*Pagrus auratus*, Sparidae) from tagging in the Shark Bay region of Western Australia. *Marine and Freshwater Research* **54**, 913-922.

Myers, R. A. (1998). When do environment-recruitment correlations work? *Reviews in Fish Biology and Fisheries* **8**, 285-305.

Myers, R. A. (2002). Recruitment: understanding density-dependence in fish populations. In 'Handbook of Fish Biology and Fisheries.' (Eds P. J. B. Hart and J. D. Reynolds.) pp. 123-148. (Blackwell Publishing: Oxford, UK.)

Myers, R. A., and Barrowman, N. J. (1996). Is fish recruitment related to spawner abundance. *Fishery Bulletin* **94**, 707-724.

Myers, R. A., and Cadigan, N. G. (1993a). Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1576-1590.

Myers, R. A., and Cadigan, N. G. (1993b). Is juvenile natural mortality in marine demersal fish variable? *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1591-1598.

Myers, R. A. Hutchings, J. A., and Barrowman, N. J. (1997). Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* **7**, 91-106.

Nelson, J.S. (2006). 'Fishes of the World. 4th Edition.' (John Wiley & Sons: New Jersey, USA.)

Nishimura, A., Hamatsu, T., Shida, O., Mihara, I., and Mutoh, T. (2007). Interannual variability in hatching period and early growth of juvenile walleye Pollock, *Theragra chalcogramma*, in the Pacific coast area of Hokkaido. *Fisheries Oceanography* **16**, 229-239.

Norris, J. V., and Jackson, G. (2002). Identifying the developmental stages of preserved eggs of snapper, *Pagrus auratus*, from Shark Bay, Western Australia, Fisheries Research Report No. 42. (Western Australian Department of Fisheries: Perth, Australia.)

Noye, J. (1984). Physical processes and pollution in the waters of Spencer Gulf. *Marine Geology* **61**, 197-220.

Nunes, R. A., and Lennon, G. W. (1986). Physical property distributions and seasonal trends in Spencer Gulf, South Australia: an inverse estuary. *Australian Journal of Marine and Freshwater Research* **37**, 39-53.

Orrell, T. M., and Carpenter, K. E. (2004). A phylogeny of the fish family Sparidae (porgies) inferred from mitochondrial sequence data. *Molecular Phylogenetics and Evolution* **32**, 425-434.

Pankhurst, P. M., Montgomery, J. C., and Pankhurst, N. W. (1991). Growth, development and behaviour of artificially reared larval *Pagrus auratus* (Bloch & Schneider, 1801) (Sparidae). *Australian Journal of Marine and Freshwater Research* **42**, 391-398.

Patzner, P. A. (2008). Reproductive strategies of fish. In 'Fish Reproduction'. (Eds M. J. Rocha, A. Arukwe and B. G. Kapoor.) pp. 311-350. (Science Publishers: New Hampshire, USA.)

Paulin, C. D. (1990). *Pagrus auratus*, a new combination for the species known as "snapper" in Australasian waters (Pisces: Sparidae). *New Zealand Journal of Marine and Freshwater Research* **24**, 259-265.

Pepin, P. and Myers, R. A. (1991). Significance of egg and larval size to recruitment variability of temperate marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1820-1828.

Petersen, C. W., Warner, R. R., Cohen, S., Hess, H. C., and Sewell, A. T. (1992). Variable pelagic fertilization success: implications for mate choice and spatial patterns of mating. *Ecology* **73**, 391-401.

Petrusevics, P. (1993). SST fronts in inverse estuaries, South Australia – indicators of reduced gulf-shelf exchange. *Australian Journal of Marine and Freshwater Research* **44**, 305-323.

Phil, L., and Van der Veer, H. W. (1992). Importance of exposure and habitat structure for the population density of 0-group plaice, *Pleuronectes platessa* L., in coastal nursery areas. *Netherlands Journal of Sea Research* **29**, 145-152.

Poore, G. C. B. (2004). 'Marine Decapod Crustacea of Southern Australia.' (CSIRO Publishing: Victoria, Australia.)

Rasero, M., González, A. F., Castro, B. G., and Guerra, A. (1996). Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Illex coindetii* Cephalopode: Ommestrephidal) in Galician waters. *Journal of the Marine Biological Association of the United Kingdom* **76**, 73–87.

Reid, A. L., and Norman, M. D. (2000). 'A Guide to Squid, Cuttlefish and Octopuses of Australasia.' (CSIRO Publishing: Victoria, Australia.)

Rhodes, K. L., and Sadovy, Y. (2002a). Reproduction in the camouflage grouper, *Epinephelus polyphekadion* (Pisces: Serranidae), in Pohnpei, Federated States of Micronesia. *Bulletin of Marine Science* **70**, 851-869.

Rhodes, K. L., and Sadovy, Y. (2002b). Temporal and spatial trends in spawning aggregations of camouflage grouper, *Epinephelus polyphekadion*, in Pohnpei, Micronesia. *Environmental Biology of Fishes* **63**, 27-39.

Rice, J. A. , Miller, T. J., Rose, K. A., Crowder, L. E., Marschall, E. A., Trebitz, A.S., and DeAngelis, D.L. (1993). Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 133-142.

Rickman, S. J., Dulvy, N. K., Jennings, S., and Reynolds, J. D. (2000). Recruitment variation related to fecundity in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 116-124.

Rideout, R.M., Rose, G.A., and Burton, M.P.M. (2005). Skipped spawning in female iteroparous fishes. *Fish and Fisheries* **6**, 50-72.

Robertson, D. R., Green, D. G., and Victor, B. C. (1988). Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. *Ecology* **69**, 370-381.

Robertson, D. R., Swearer, S. E., Kaufman, K., and Brothers, E. B. (1999). Settlement vs. environmental dynamics in a pelagic-spawning reef fish at Caribbean Panama. *Ecological Monographs* **69**, 195-218.

Ross, P. M., Thrush, S. F., Montgomery, J. C., Walker, J. W. and Parsons, D. M (2007). Habitat complexity and predation risk determine juvenile snapper (*Pagrus auratus*) and goatfish (*Upeneichthys lineatus*) behaviour and distribution. *Marine and Freshwater Research* **58**, 1144–1151

Rothschild, B. J. (1986). ‘Dynamics of marine fish populations.’ (Harvard University Press: Massachusetts, USA.)

Rothschild, B. J. (2000). "Fish stocks and recruitment": the past thirty years. *ICES Journal of Marine Science* **57**, 191-201.

Roughgarden, J., Gaines, S.D., and Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science* **241**, 1460-1466.

Sale, P. F. (1990). Recruitment of marine species: Is the bandwagon rolling in the right direction? *Trends in Ecology & Evolution* **5**, 25-27.

Sanders, M. J. (1974). Tagging indicates at least two stocks of snapper *Chrysophrys auratus* in south-east Australian waters. *New Zealand Journal of Marine and Freshwater Research* **8**, 371-374.

Scott, S. G., and Pankhurst, N. W. (1992). Interannual variation in the reproductive cycle of the New Zealand snapper *Pagrus auratus* (Bloch & Schneider) (Sparidae). *Journal of Fish Biology* **41**, 685-696.

Scott, S. G., Zeldis, J. R., and Pankhurst, N. W. (1993). Evidence of daily spawning in natural populations of the New Zealand snapper *Pagrus auratus* (Sparidae). *Environmental Biology of Fishes* **36**, 149-156.

Secor, D. (2007). The year-class strength phenomenon and the storage effect in marine fishes. *Journal of Sea Research* **57**, 91-103.

Sheaves, M. (2006). Is the timing of spawning in sparid fishes a response to sea temperature regimes? *Coral Reefs* **25**, 655-669.

Shepherd J. G., and Cushing D.H. (1981). A mechanism for density dependent survival of 1arval fish as the basis of a stock recruitment relationship. *Journal du Conseil International pour l'Exploration de la Mer* **39**,160-167.

Shepherd, S. A. (1983). Benthic communities of upper Spencer Gulf, South Australia. *Transactions of the Royal Society of South Australia* **107**, 69-85.

Shepherd, S. A., and Thomas, I. M. (1982). 'Marine Invertebrates of Southern Australia. Part 1.' (Government Printer: Adelaide, Australia.)

Shoji, J., Sakiyama, K., Hori, M., Yoshida, G., and Hamaguchi, M. (2007). Seagrass habitat reduces vulnerability of red sea bream *Pagrus major* juveniles to piscivorous fish predator. *Fisheries Science* **73**, 1281-1285.

Sigler, M. F., Hulbert, L. B., Lunsford, C. R., Thompson, N. H., Burek, K., O'Corry-Crowe, G., and Hirons, A. C. (2006). Diet of Pacific sleeper shark, a potential Steller sea lion predator, in the north-east Pacific Ocean *Journal of Fish Biology* **69**, 392 - 405.

Sinclair, M. (1988). 'Marine Populations. An Essay on Population Regulation and Speciation.' (University of Washington Press: Seattle, USA.)

Sinclair, M. (1997). Prologue. Recruitment in fish populations: the paradigm shift generated by ICES Committee A. In 'Early Life History and Recruitment in Fish Populations'. (Eds R. C. Chambers and E. A. Trippel) pp 1-27. (Chapman & Hall: London, UK.)

Sissenwine, M. P. (1984). Why do fish populations vary? In 'Exploitation of Marine Communities' (Ed. R. M. May.) pp. 59-94. (Springer-Verlag: Berlin, Germany.)

Smith, M. M., and Heemstra, P. C. (1986). 'Smiths' Sea Fishes.' (MacMillan: Johannesburg, South Africa.)

Sogard, S. M., Able, K. W., and Hagen, S. M. (2001). Long-term assessment of settlement and growth of juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. *Journal of Sea Research* **45**, 189-204.

Somarakis, S., Ganias, K., Tserpes, T., and Koutsikopoulos, G. (2004). Ovarian allometry and the use of the gonosomatic index: a case study in the Mediterranean sardine *Sardina pilchardus*. *Marine Biology* **146**, 181-189.

Sponaugle, S., and Pinkhard, D. (2004). Lunar cyclic population replenishment of a coral reef fish: shifting patterns following oceanic events. *Marine Ecology Progress Series* **267**, 267-280.

Sudo, H., and Azeta, M. (2001). The microhabitat and size of gammarid species selectively predated by young red sea bream *Pagrus major*. *Fisheries Science* **67**, 389-400.

Sudo, H. Ikemoto, R., and Azeta, M. (1983). Studies on habitat quality evaluation of young red sea bream in Shijiki Bay. *Bulletin of the Seikai Regional Fisheries Research Laboratory* **59**, 71-84.

Sudo, H., Azuma, M., and Azeta, M. (1987). Diel changes in predator-prey relationships between red sea bream and gammaridean amphipods in Shijiki Bay. *Nippon Suisan Gakkaishi* **53**, 1567-1575.

Sullivan, M. C., Cowen, R. K., Able, K. W., and Fahay, M. P. (2000). Spatial scaling of recruitment in four continental shelf fishes. *Marine Ecology Progress Series* **207**, 141-154.

Sumpton, W., and Jackson, S. (2005). The effects of incidental trawl capture of juvenile snapper (*Pagrus auratus*) on yield of a sub-tropical line fishery in Australia: an assessment examining habitat preference and early life history characteristics. *Fisheries Research* **71**, 335-347.

Tabata, K., and Taniguchi, N. (2000). Differences between *Pagrus major* and *Pagrus auratus* through mainly mtDNA control region analysis. *Fisheries Science* **66**, 9-18.

Tanaka, M. (1985). Factors affecting the inshore migration of pelagic larval and demersal juvenile red sea bream *Pagrus major* to a Nursery ground. *Transactions of the American Fisheries Society* **114**, 471-477.

Thrush, S. F., Schultz, D., Hewitt, J. E., and Talley, D. (2002). Habitat structure in soft-sediment environments and abundance of juvenile snapper *Pagrus auratus*. *Marine Ecology Progress Series* **245**, 273-280.

Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. *BioScience* **45**, 759-771.

Trnski, T. (2002). Behaviour of settlement-stage larvae of fishes with an estuarine juvenile phase: in situ observations in a warm-temperate estuary. *Marine Ecology Progress Series* **242**, 205-214.

Tupper, M., and Boutilier, R. G. (1995). Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. *Marine Ecology Progress Series* **118**, 295-300.

Underwood, A. J. (1997). 'Experiments in Ecology.' (Cambridge University Press, Cambridge, UK.)

Victor, B.C. (1983). Recruitment and population dynamics of a coral reef fish. *Science* **219**, 419-420.

Vinagre, C., Cabral, H., and Costa, M. J. (2008). Prey selection by flounder, *Platichthys flesus*, in the Douro estuary, Portugal. *Journal of Applied Ichthyology* **24**, 238-243.

Wennhage, H. (2002). Vulnerability of newly settled plaice (*Pleuronectes platessa* L.) to predation: effects of habitat structure and predator functional response. *Journal of Experimental Marine Biology and Ecology* **269**, 129-145.

Wennhage, H., and Gibson, R. N. (1998). Influence of food supply and a potential predator (*Crangon crangon*) on settling behaviour of plaice (*Pleuronectes platessa*). *Journal of Sea Research* **39**, 103-112.

Werner, F. E., Quinlan, J. A., Blanton, B. O., and Leuttich, R. A. (1997). The role of hydrodynamics in explaining variability in fish populations. *Journal of Sea Research* **37**, 195-212.

Winemiller, K.O., and Rose, K.A. (1993). Why do fish produce so many tiny offspring? *The American Naturalist* **142**, 585-603.

Witthames, P. R., and Marshall, C. T. (2008). The importance of reproductive dynamics in fish stock assessments. In 'Advances in Fisheries Science. 50 years on from Beverton and Holt'. (Eds A. Payne, J. Cotter and T. Potter.) pp. 306-324. (Blackwell Publishing: Oxford, UK.)

Wright, P. J., and Bailey, M. C. (1996). Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. *Marine Biology* **126**, 143-152.

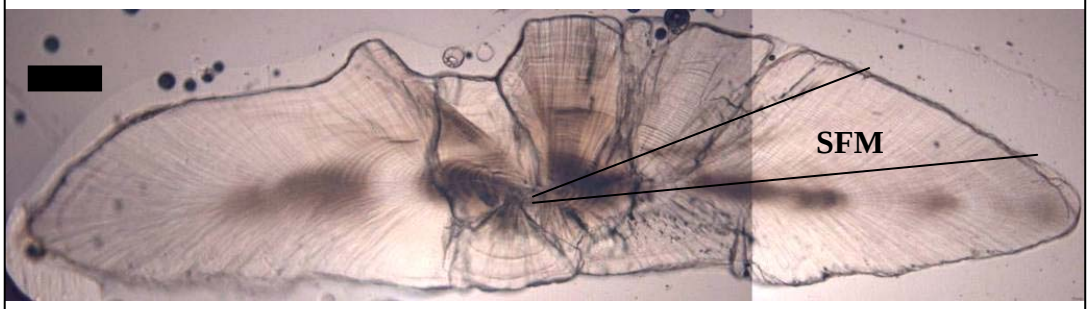
Wright, P. J., and Gibb, F. M. (2005). Selection for birth date in North Sea haddock and its relation to maternal age. *Journal of Animal Ecology* **74**, 303-312.

Zar, J. H. (1999). 'Biostatistical Analysis.' (Prentice Hall: Upper Saddle River, USA.)

Zeldis, J. R., and Francis, R. (1998). A daily egg production method estimate of snapper biomass in Hauraki Gulf, New Zealand. *ICES Journal of Marine Science* **55**, 522-534.

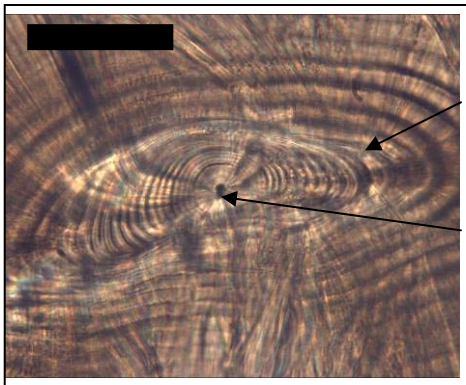
Appendix 1
Digital images of sagittal section of an otolith from a 0+ snapper of 55mm fork length. Scale bar: 50µm in all cases.

PROXIMAL

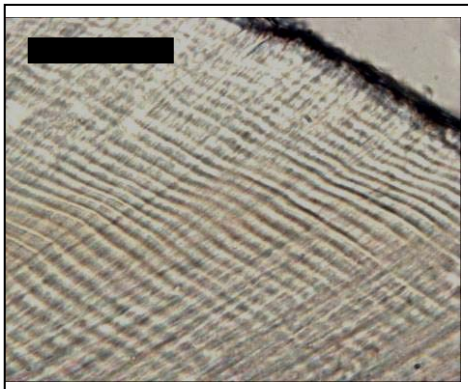


DORSAL DISTAL VENTRAL

Transverse section of a 0+ snapper otolith (composite image) at 10x magnification. The borders of the subcupular meshwork fibre zone (SFM) are delineated by black lines on the image above and follow (Francis 1994b).



Central portion of otolith from 0+ snapper showing settlement mark and primordium at 1000x magnification. (orientation is the same as above image)



Edge of 0+ snapper otolith showing increments towards the edge of the otolith at 1000x magnification. (orientation is the same as the above image)

Appendix 2. Summary table of all fish and macro-invertebrates captured. Frequency is the percent of trawls that contained the species and abundance is the total number caught in all trawls.

Classification	Scientific name	Common name	Abundance	Frequency
cephalopod				
Octopoda				
Octopodidae				
	Octopus spp	octopus	35	18.3
Sepiida				
Sepiadariidae				
	Sepioloidea lineolata	pinstripe bottle-tailed squid	12	5.6
Sepiidae				
	Sepia apama	giant cuttlefish	26	12.7
	Sepia novaehollandiae	cuttlefish	26	13.4
Sepiolida				
Sepiolidae				
	Euprymna tasmanica	southern dumpling squid	47	25.4
	Sepiola sp	southern bobtail squid	1	0.7
Teuthida				
Loliginidae				
	Sepioteuthis australis	southern calamari	53	23.2
crustacean				
Decapoda				
Corystidae				
	Gomeza bicornis	masked burrowing crab	11	1.4
Dromiidae				
	Austrodromidia octodentata	bristled sponge crab	1	0.7
	Lamarckdromia globosa	fringed sponge crab	1	0.7
	Stimdromia lamellata	sponge crab	1	0.7
	Stimdromia lateralis	ridged sponge crab	5	2.1
Goneplacidae				
	Litocheira bispinosa	two-spined slender-clawed crab	3	2.1
Hymenosomatidae				
	Halicarcinus ovatus	three-pronged flat spider crab	1	0.7
	Trigonoplax longirostris	flat spider crab	1	0.7
Leucosiidae				
	Bellidilia laevis	smooth pebble crab	2	0.7
Majidae				
	Dumea latipes	velvet crab	1	0.7
	Huenia australis	spider crab a	1	0.7
	Naxia aurita	golden decorator crab	1	0.7
	Schizophrys rufescens	spider crab b	2	1.4
Penaeidae				
	Metapenaeopsis lindae	strawberry prawn	715	31.7
	Penaeus latisulcatus	western king prawn	9411	83.8
Pilumnidae				
	Pilumnus monilifer	bearded hairy crab	1	0.7
	Pilumnus tomentosus	common hairy crab	23	8.5
Portunidae				
	Nectocarcinus integrifrons	rough rock crab	4	2.8
	Portunus pelagicus	blue swimmer crab	1986	82.4
Xanthidae				
	Zalasius australis	long-haired crab	2	1.4
Stomatopoda				
Squillidae				
	Belosquilla laevis	prawn killer	545	62
elasmobranch				
Heterodontiformes				
Heterodontidae				
	Heterodontus portusjacksoni	Port Jackson shark	1	0.7
Orectolobiformes				
Orectolobidae				
	Sutorectus tentaculatus	cobbler wobbegong	2	1.4
Torpediniformes				
Torpedinidae				
	Hypnos monopterygium	coffin ray	1	0.7

Appendix 2. continued

Classification	Scientific name	Common name	Abundance	Frequency
teleost				
Atheriniformes				
Atherinidae				
	Atherinason hepsetoides	smallscale hardyhead	39	4.2
Beloniformes				
Hemiramphidae				
	Hyporhamphus melanochir	southern garfish	299	30.3
Clupeiformes				
Clupeidae				
	Spratelloides robustus	blue sprat	69	19.7
Engraulidae				
	Engraulis australis	Australian anchovy	158	29.6
Lophiiformes				
Antennariidae				
	Rhycherus gloveri	Glover's anglerfish	14	8.5
Ophidiiformes				
Bythitidae				
	Dermatopsis multiradiatus	slender blindfish	8	4.9
Perciformes				
Apogonidae				
	Siphamia cephalotes	Wood's siphonfish	1519	48.6
	Vincentia badia	scarlet cardinalfish	199	13.4
	Vincentia conspersa	southern cardinalfish	1051	58.5
Arripidae				
	Arripis truttaceus	west Australian salmon	1	0.7
Callionymidae				
	Eocallionymus papilio	painted stinkfish	10	4.9
	Repomucenus calcaratus	spotted dragonet	899	65.5
Carangidae				
	Pseudocaranx wrighti	skipjack trevally	169	40.8
Clinidae				
	Cristiceps australis	southern crested weedfish	34	13.4
	Heteroclinus adelaidae	Adelaide weedfish	7	1.4
	Heteroclinus macrophthalmus	large-eye weedfish	12	3.5
	Heteroclinus sp	a weedfish	24	2.1
	Heteroclinus sp 5	fewray weedfish	10	3.5
	Ophiclinops pardalis	spotted snake blenny	3	1.4
	Ophiclinops sp	a snake blenny	4	1.4
	Ophiclinus antarcticus	dusky snake blenny	112	33.8
	Ophiclinus sp	a snake blenny	4	2.8
	Peronedys anguillaris	eel snake blenny	1	0.7
Gerreidae				
	Parequula melbournensis	silverbelly	58	14.8
Gobiidae				
	Arenigobius bifrenatus	bridled goby	56	7.7
	Bathygobius krefftii	frill goby	7	3.5
	Callogobius mucosus	sculptured goby	26	10.6
	Favonigobius lateralis	southern longfin goby	218	23.9
	Nesogobius pulchellus	sailfin goby	197	13.4
	Nesogobius sp	a goby	40	5.6
	Nesogobius sp 2	threadfin sandgoby	472	35.2
	Pseudogobius olorum	bluespot goby	4	0.7
	Tasmanogobius gloveri	Glover's tasmangoby	99	15.5
Mullidae				
	Upeneichthys vlamingii	bluespotted goatfish	214	35.9
Odacidae				
	Haletta semifasciata	blue weed whiting	9	3.5
	Neoodax balteatus	little weed whiting	304	21.8
	Siphonognathus attenuatus	slender weed whiting	52	14.8
	Siphonognathus radiatus	longray weed whiting	1087	12
Parapercidae				
	Parapercis haackei	wavy grubfish	4578	93.7
Pempheridae				
	Parapriacanthus elongatus	elongate bullseye	11	3.5
Sillaginidae				
	Sillaginodes punctatus	King George whiting	10	7
Sparidae				
	Chrysophrys auratus	Snapper	81	26.8
Sphyraenidae				
	Sphyraena novaehollandiae	snook	14	5.6
Terapontidae				
	Pelates octolineatus	western striped grunter	145	29.6

Appendix 2. continued

Classification	Scientific name	Common name	Abundance	Frequency
teleost				
Pleuronectiformes				
Cynoglossidae				
	Cynoglossus broadhursti	southern tongue sole	2	1.4
Paralichthyidae				
	Pseudorhombus jenynsii	smalltooth flathead	71	28.9
Pleuronectidae				
	Ammotretis elongatus	elongate flounder	1	0.7
Scorpaeniformes				
Aploactinidae				
	Acanthosphex (?) sp	a velvetfish	6	3.5
	Kanekonia queenslandica	deep velvetfish	5	3.5
	Neoaploactis tridorsalis	threefin velvetfish	4	2.8
Neosebastidae				
	Maxillicosta scabriceps	little gurnard perch	16	7
Platycephalidae				
	Leviprora inops	longhead flathead	2	0.7
	Platycephalus bassensis	southern sand flathead	14	7
	Platycephalus laevigatus	rock flathead	3	1.4
	Platycephalus speculator	southern bluespotted flathead	21	12.7
Tetrarogidae				
	Glyptauchen panduratus	goblinfish	3	2.1
	Gymnapistes marmoratus	soldierfish	376	45.8
Triglidae				
	Lepidotrigla papilio	spiny gurnard	13	6.3
Siluriformes				
Plotosidae				
	Cnidoglanis macrocephalus	estuary cobbler	1	0.7
Sygnathiformes				
Syngnathidae				
	Filicampus tigris	tiger pipefish	23	10.6
	Hippocampus abdominalis	bigbelly seahorse	6	4.2
	Hippocampus breviceps	shorthead seahorse	2	1.4
	Histiogamphelus cristatus	rhino pipefish	3	2.1
	Leptoichthys fistularius	brushtail pipefish	234	7
	Pugnaso curtirostris	pugnose pipefish	1	0.7
	Stigmatopora argus	spotted pipefish	1822	21.1
	Stigmatopora narinosa	gulf pipefish	3	2.1
	Stigmatopora nigra	widebody pipefish	46	3.5
	Vanacampus phillipi	Port Phillip pipefish	82	19
	Vanacampus vercoi	Verco's pipefish	5	0.7
Tetraodontiformes				
Diodontidae				
	Diodon nicthemerus	globefish	12	7
Monacanthidae				
	Acanthaluteres spilomelanurus	bridled leatherjacket	1005	54.2
	Brachaluteres jacksonianus	southern pygmy leatherjacket	336	62.7
	Scobinichthys granulatus	rough leatherjacket	384	31
	Thamnaconus degenii	bluefin leatherjacket	5	3.5
Ostraciidae				
	Aracana aurita	shaw's cowfish	3	2.1
Tetraodontidae				
	Contusus richei	barred toadfish	1	0.7
	Torquigener pleurogramma	weeping toadfish	13	3.5