Fisheries

A synthesis of fishery and biological information for Snapper (*Chrysophrys auratus*) in South Australia

AJ Fowler

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SARDI
SOUTH AUSTRALIAN RESEARCH AND DEVELOPMENT INSTITUTE

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ACKNOWLEDGEMENTS

I appreciate having been given the rare opportunity to review the numerous research projects that have been undertaken on Snapper in South Australia over the past 20 years or so, and to consider their outcomes in the context of the earlier work done over the preceding 30 years. The process has resulted in some amazing insights which are evident throughout the report but mostly in the final chapter, which is a culmination of everything that has come beforehand. The need for the project became apparent during the latter 2000s from some challenges that were faced by SARDI's Snapper research team when undertaking stock assessments. The idea for the project was supported by SARDI who allowed me to work on it during the final period of my employment and more recently as a Visiting Scientist.

This report, the culmination of the project, is dedicated to the scientists and many technical staff who worked on Snapper projects in South Australia over the past 50 years or so. There are too many to name individually, but most have been acknowledged in the many reports and publications that were produced through this time. Nevertheless, some people made notable contributions and deserve particular recognition. Dr Keith Jones was the pioneer of Snapper research in South Australia. In the late 1970s and 1980s, he initiated market sampling and fish ageing, and undertook significant tag/recapture projects. In the 1990s, Dr David McGlennon continued this work and expanded the focus to include the early life history and recruitment as well as pioneering the use of the DEPM for estimating spawning biomass of Snapper in South Australia. The legacy of these scientists was the knowledge base and suite of methodologies that were available to the Snapper research team in the early 2000s when there was renewed focus on this species, which has become progressively more intense as the 2000s progressed. Throughout the 1990s and 2000s until 2016, Bruce Jackson was the stalwart of the research team making many significant and diverse contributions. The tangible legacy of his work is the thousands of otoliths from adult Snapper that were collected and aged from across the State. In the future this archive will continue to be an invaluable resource.

Through the early and mid-2000s, the different members of the Snapper research team contributed to the market sampling work and to the annual recruitment surveys. Some, however, made further contributions. Paul Jennings developed the methodology for ageing juvenile Snapper and over several years aged hundreds of such fish. Dr Karina Hall managed the first otolith chemistry study that ultimately proved to be invaluable. Dr Richard Saunders joined the Snapper research team as a PhD student and contributed numerous insights in relation to reproductive biology, early life history and recruitment dynamics. Matthew Lloyd and Dr Charlie Huveneers ran the acoustic tagging projects that were informative about the movement behaviour of adult Snapper. Furthermore, Matt's Honours research project on the dietary diversity of Snapper was another significant empirical contribution. In the latter 2000s, the DEPM became a significant component of Snapper stock assessments. Important contributions to the development of this methodology and its application and to the ecology of the early life history stages were made by Dr Michael Steer, Dr Michael Drew, Dr Troy Rogers and Damian Matthews. Throughout the 2000s, an invaluable component of the stock assessment processes has been the SnapEst computer fishery model, which was developed by Dr Rick McGarvey and his team. They have continued to refine this model through various iterations as the stock assessment processes have changed and become more sophisticated.

Through the numerous eras of research and many projects on Snapper, there have been many research cruises undertaken on the MRV Ngerin. The understanding that we now have about the life history and population biology of Snapper would not have been possible without the devotion and professionalism of the different crews of the vessel.

The scientific research on Snapper over the past 50 years would not have been possible without financial support. SARDI and PIRSA have continued to recognise this species as a significant fishery resource for South Australia and have directed important resources to the continuation of appropriate projects. Also, through the 1990s and particularly through the 2000s, the Fisheries Research and Development Corporation has provided significant financial support for projects on this species in southern Australia.

I would finally like to express appreciation to several people. They include Drs David McGlennon, Owen Burnell and Craig Noell who provided access to some raw data. Jamie Crawford provided the photo of the adult Snapper on the title page. Discussions with Dr Heidi Alleway helped me appreciate the significance of historical ecology and provided copies of several documents that related to the history of Snapper fishing in South Australia. Also, over the years I have had many discussions about research methodologies and the interpretation of research findings for the biology of the species and management of its fisheries. These include Dr Rick McGarvey, Bruce Jackson, Paul Jennings, Dr Richard Saunders, Dr Mick Drew and Dr Mike Steer. In recent years, the latter group has included Dr Troy Rogers, who has been an important sounding board for my ideas on the functionality of Snapper populations and the demographic processes that drive their population dynamics. Finally, I express my appreciation to Drs Troy Rogers, Mick Drew, Craig Noell and to Dr Stephen Mayfield who undertook the onerous task of reviewing the various chapters of the report. Their input has contributed considerably to improving the presentation and content of the report.

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EXECUTIVE SUMMARY

Background

Snapper (*Chrysophrys auratus*) is an iconic marine finfish species throughout Australasia. As each Australian mainland State supports important commercial, recreational and charter boat fisheries, it is one of Australia's most significant fishery resources. Around the start of the 21st Century, the State of South Australia was producing the highest State-based commercial catches, as well as high recreational catches. Since then, there have been significant changes in the fishery. From 2010, the State-wide catches declined to their lowest levels since the early 1960s, associated with reductions in biomass. These declines in fishery production led to downgrades in the stock statuses that were assigned in stock assessments. Furthermore, there were significant changes in the spatial structure of the fishery, evident as rolling changes from region to region in the timing of the reductions. From 2010, numerous management changes were implemented to try to arrest the declines. These, however, did not work. Consequently, in November 2019, the two main Snapper fisheries in South Australia's gulfs and the west coast of Eyre Peninsula were closed to fishing.

During the 21st Century, the concern about South Australia's Snapper fishery led to a significant investment in scientific effort directed towards understanding the declines in biomass, the changes in regional, spatial structure and to improve approaches to stock assessment and fishery management. The intensity in scientific research increased with the resulting outcomes and understanding, which added to the knowledge that had accumulated through research that had been undertaken since the mid-1970s. This accumulated knowledge on the life history and population biology of Snapper in South Australia was disparate and difficult to access, as much had not yet been reported in the primary literature. This report has collated this information and understanding, providing a resource to facilitate research and management of the fishery. It should be useful for current and future researchers in South Australia, those in other jurisdictions, and would also likely be a useful reference for fishery managers and fishing industry representatives.

The twelve chapters of the report begin with a description of the development and the history of the South Australian Snapper fishery. The bulk of the report is focussed on ecological studies that have revealed the spatial and temporal aspects of the different life history stages and the biological processes that maintain the populations. The topics include: the reproductive biology; the development of the eggs and larvae and their spatial patterns of distribution an abundance; the inter-annual variation in recruitment of the juvenile fish and its causes; the biology of the adult fish based on ageing fish from their otoliths and movement behaviour determined by acoustic telemetry; and the connectivity amongst populations and stock structure determined from genetic and otolith chemistry studies. Ultimately, the report concludes with a description of the demographic processes

that occurred through the 1990s and 2000s that ultimately led to the declines in stocks and classifications of stock status that eventually warranted the closure of the fisheries.

History of the fishery

Chapter 1 considered the development of the regional Snapper fisheries in South Australia and the possible effects that fishing may have had on the populations. The purpose was to investigate what Snapper populations may have been like historically to provide a broader historical context from which to consider and manage the modern-day fisheries. It provided a historical description of the fishery, presented the time series of State-wide commercial catches from 1951 to 2019, as well as detailed fishery data from 1984 onwards, including a comprehensive, regional breakdown of commercial fishery statistics. Also included is a largely anecdotal description of the development of the recreational sector that included estimates of recreational catches from four State-wide surveys from the early 1990s onwards.

Prior to the closures of South Australia's fisheries in 2019, the populations had likely been fished for thousands of years. However, since colonisation approximately 200 years ago, targeted effort would have increased enormously as the commercial and recreational sectors developed, and the technology available to all fishers increased their capability to find and to catch Snapper. It was possible to speculate in a qualitative sense about how catches changed over time, but more difficult to determine the effects on populations. There is better understanding for the more recent years of the fishery. The high catches taken during the first decade of the 2000s are likely the highest level of human extraction from South Australia's Snapper populations. They contributed to reductions in biomass at the regional scale, and the progression amongst regions in declines in fishery production. The way that this occurred demographically was spatially complex. The following chapters summarise the developments in understanding of the life history and the ecological aspects of the population biology that helped understand the regional declines in fishery production.

Reproductive biology

Through the latter 2000s, the daily egg production method (DEPM) for estimating spawning biomass has become an important component of the stock assessment process for Snapper in South Australia. Estimates of 'spawning fraction' constitute one of the primary adult parameters required for the estimations. Chapter 2 provided basic information about classifying the maturity stages of female Snapper, from which the estimates of spawning fraction were derived. Then it collated historical estimates of spawning fraction for Northern Spencer Gulf (NSG), from studies done during the 1990s, the early, mid and late-2000s, and estimates for the summers of 2019/20 and 2021/22 for Southern Spencer Gulf (SSG), and Northern and Southern Gulf St. Vincent (NGSV, SGSV). The estimates of spawning fraction demonstrated considerable within-region temporal variability. This was thought to at least partly involve a component of spatial variation that related to an influence of habitat on gonad maturation and spawning. This implies a confounding between spatial and temporal influences over maturation and spawning. The implications of resolving such confounding by appropriate sampling of adult fish were discussed.

The focus of Chapter 3 was on describing the regional variation in the phenology of the reproductive biology of Snapper in South Australia, in the context of the timing of reproduction in other Australasian regions. The focus was to identify the environmental conditions to which the seasonality in reproductive biology might be entrained. The regional comparison that involved NSG, SSG, NGSV and SGSV indicated that the timing of pre-spawning development and onset of spawning did not vary regionally. However, the durations of the spawning seasons did vary. This suggests that the physiological processes involved in reproductive maturation for Snapper in South Australia were strongly influenced by regional SST regimes. A similar conclusion was drawn from the broader latitudinal consideration of the timing of reproductive maturation and spawning. The differences in timing with latitude had the consequences that, regardless of place, the eggs and larvae would be exposed to a narrower range of environmental conditions compared to those experienced by the adults throughout their range. Lab-rearing experiments had suggested that the optimal temperature range for survivorship of Snapper eggs and larvae was 18-22°C. With environmental conditions changing throughout Australia’s coastal waters because of climate change, in the future this is likely to have significant implications for the viability of populations in sub-tropical regions, whilst the extension of populations into colder temperate regions continues.

Ecology of early life history stages

Chapter 4 was concerned with collating and summarising the results from Snapper egg surveys that have been undertaken in South Australia. Such surveys had been done in the mid-1990s, the early 2000s, and more recently during the mid-late 2010s. Each survey was associated with an application of the DEPM, to provide an estimate of spawning biomass for NSG and more recently for Gulf St. Vincent (GSV) and Investigator Strait (IS). Such applications depend on accurate identification and enumeration of Snapper eggs in wild plankton samples. This identification has generally relied on the morphological characteristics of the eggs, requiring an understanding of the development and morphological characteristics of Snapper eggs. Then, the results from the various plankton surveys were summarised, including; the locations of stations, the volumes of water sampled, and the numbers and densities of Snapper eggs captured. In general, the latter were low when compared with results from similar surveys undertaken elsewhere in Australasia.

Chapter 5 focussed on the larval stage of the life history. Studies done elsewhere had established that it is during the early larval stage that year class strength is established. Here, information was integrated from several sources. A development series for the larvae was generated from tank-reared specimens at South Australian Aquatic Sciences Centre (SAASC). Understanding about the development of the swimming capability of larvae and their diurnal vertical migration were gleaned from the literature, to later contribute to developing a biophysical model to consider the capability of dispersion during the early life history. The growth of the larvae was described from the analysis of the microstructure of otoliths from juvenile fish captured in NSG. The patterns of distribution and abundance of Snapper larvae were determined from the plankton samples collected during egg surveys for DEPMs. Overall, the numbers of Snapper larvae captured were low, particularly for Spencer Gulf. Throughout the 2000s, the waters of NSG, GSV and IS were depauperate of Snapper larvae, compared with similar surveys done elsewhere throughout Australasia.

Chapter 6 collated and summarised results from studies on the recruitment rates of juvenile fish. In South Australia, such inter-annual variability drives the population dynamics for Snapper populations, so having an annual index of recruitment could be an invaluable predictor of future adult biomass and fishery productivity. For Spencer Gulf, two types of studies have provided spatial and temporal information for juvenile Snapper. Between 2000 and 2010, otter trawl surveys were undertaken annually in NSG, producing estimates of density for both the 0+ and 1+ year classes of juvenile Snapper, and their spatial dispersion. The densities of the 0+ fish were highly variable from year-to-year, although they were consistently captured in specific areas in the northern part of the region. These areas supported a muddy substratum, as distinct from more extensive areas of coarse sand and gravel. The densities of the 1+ fish also demonstrated considerable inter-annual variability. These fish were aggregated, possibly around reef structure, and were located further south than the 0+ fish, suggesting some movement since settlement. The second type of study that informed about juvenile Snapper were by-catch surveys for the Spencer Gulf Prawn Fishery, done since the early 1990s. These surveys extended into SSG, and so were more spatially extensive than the otter trawl surveys. They demonstrated that most juveniles were captured in the northern gulf, indicating the significance of the nursery areas of this region. In different years the capture rates were consistent with strong and weak year classes that were identified from population age structures. This supports the notion that data from prawn by-catch surveys could provide a valuable early indicator of year class strength for Snapper in the gulfs.

For Snapper, historically there has been considerable interest in understanding the causes of the temporal variation in recruitment. Chapter 7 explored the relationship between recruitment variability and potential environmental influences. The recruitment time series considered were those generated for the Spencer Gulf/West Coast Stock (SG/WCS) and the Gulf St. Vincent Stock (GSVS) by the SnapEst model for the stock assessment in 2020. The time series covered the 35-year period from 1983 to 2017. The physical environmental data included sea surface temperature accessed from satellite imagery, as well as wind and rain data from the Bureau of Meteorology. Correlation analyses compared the biological and physical environmental datasets. For the SG/WCS, there were up to five strong year classes throughout the 35-year period. These did not correspond to any obvious weather patterns and there were no significant correlations with environmental variables. For the GSVS, there were more strong year classes in the recruitment time series, as well as several significant correlations with the environmental datasets. The contrasting outcomes for the two stocks indicate that recruitment variability for Snapper in South Australia is not driven simply by a single environmental variable, but rather is likely to involve a complex combination of multiple factors. This is consistent with outcomes from other studies done elsewhere that demonstrated that the vulnerability to starvation of newly hatched Snapper larvae depends on the taxa and abundances of zooplankton available as food that vary between years.

Chapter 8 maintained the focus on understanding the inter-annual variation in recruitment. It was conceptually based on the likelihood that year class strength is established during the early life history. It provided insight into this life history stage, and aspects of the larval and juvenile ecology through the retrospective interpretation of the microstructure of the otoliths of juvenile Snapper that were captured during the otter trawl surveys in NSG between 2000 and 2010. From the pre-settlement and post-settlement daily micro-increments in the TS-sections of the sagittae, estimates of age and pre-settlement duration in days were determined. In association with the date-of-capture, these estimates were used to calculate the dates on which each fish was spawned, when it hatched from the egg, and when it settled to the benthic habitat in the nursery areas. The timing of these early life history processes and events were compared amongst years and considered in the context of inter-annual environmental differences. From these inter-annual comparisons, it emerged that most successful recruits to NSG were spawned in December or January, but the actual timing varied considerably amongst years. The variation in timing of spawning that led to successful recruitment related to when the SSTs in NSG increased through the range of 22 to 25°C. This established a possible link between the physical environment and physiological tolerance limits on the survivorship and development of Snapper eggs and larvae. The limited period during which the SSTs are in this range may restrict the ‘window of opportunity’ for survivorship of the eggs and larvae, which thereby affects the possibility of production of a strong year class.

Adult biology, age-based parameters, regional connectivity, movement, stock structure

Determining the ages of samples of adult fish provides fundamental information on how populations work and allows estimation of rates of demographic processes. Developing a fish ageing protocol for which there can be confidence in the assigned estimates of age requires validation of the ageing methodology and consideration of the quality assurance (QA) and quality control (QC) procedures. Chapter 9 considered the chronology of adult ageing studies that have been done for Snapper in South Australia. The ageing methods and considerations towards validation and QA/QC procedures were described. It also provided a summary of the age-related information at the regional spatial scale collected throughout the 2000s. Ageing work for Snapper in South Australia commenced nearly 50 years ago and was originally based on the structure of fish scales. By the early 1990s, concerns had emerged about the accuracy of such age estimates. Since then, the ageing of Snapper has been done using the TS-sections of the sagittae, the largest pair of otoliths. Confidence can be placed in the resulting age estimates. Validation work has demonstrated that the otolith sections display an alternating sequence of opaque and translucent zones that are formed annually throughout the fish's lives. Through the 2000s, >20,000 Snapper from across South Australian waters have been aged. Since 2008, a reference collection of TS-sections has been used for training purposes and to ensure that otolith structure is interpreted consistently. Population age structures have been developed approximately annually at the regional scale. They demonstrate considerable variation in year class strength, the consequence of variable recruitment. Differences in age structures at the regional scale indicated different timing in recruitment patterns. The rates of growth and estimates of longevity also varied considerably amongst regions.

For fishery species it is important to understand the stock structure as it determines the spatial scale at which fishery assessment and management should be directed. Achieving this is complex and challenging. Chapter 10 was focussed on the chronology of four studies done since the mid-1990s for Snapper in the south-eastern geographic region of Australia. These provided insights into the connectivity amongst regional populations and informed about stock structure. Two genetic studies were done approximately 25 years apart that applied very different technical methodologies. The other two studies were done during the early and mid-2000s and involved similar comparisons of phenotypic characteristics amongst regional populations, including age-related data on otolith chemistry from analyses of TS-sections of otoliths using laser ablation inductively coupled plasma mass spectrometry. The latter data indicate that throughout south-eastern Australia, there are only two or three primary nursery areas and recruitment to them demonstrates high inter-annual variability. Several years after recruitment of a strong year class, there is density dependent, age-related emigration over distances of hundreds of kilometres that leads to replenishment of adjacent and distance regional populations. Based on such connectivity amongst regional populations, South Australian Snapper were proposed to involve three stocks; the Spencer Gulf/West Coast Stock, Gulf St. Vincent Stock and the Western Victorian Stock. There is evidence that their boundaries overlap, with some mixing of individuals from different natal origins.

For fishery species, understanding space use and movement behaviour is necessary for developing appropriate fishery management strategies. Chapter 11 describes two acoustic telemetry studies that were done for Snapper in South Australia to describe movement behaviour; the first done in NSG in 2009 and the second done in NGSV between 2011 and 2014. They demonstrated that Snapper were relatively sedentary and site-attached for considerable periods, but that such behaviour was not consistent as ultimately fish moved away from aggregation sites. Several types of space use were identified based on different categories of fish movement that varied in their spatial and temporal scales. These movement behaviours were; inter-regional, seasonal, local and episodic. Some fish moved over distances of tens of kms, and their activity patterns were distributed

over areas of hundreds of square kms. Snapper proved to be highly mobile, exhibiting systematic behaviour at several temporal scales and demonstrated refined abilities of navigation.

Recent regional population dynamics

Regional population dynamics in South Australia's Snapper fishery are driven by inter-annual variation in recruitment and density dependent migration from nursery areas to adjacent and distant regions. Through the 2000s, there were significant changes to the spatial structure of the fishery that related to changes in biomass associated with the recruitment of strong year classes and subsequent inter-regional migration. Chapter 12 focussed on the timing of the demographic processes as they occurred for the regional populations of the Spencer Gulf/West Coast Stock, Gulf St. Vincent Stock and for the SE Region. Estimates of biomass and annual recruitment rates were output from the SnapEst model in 2020. Results from otolith chemistry analyses identified the natal origins of strong year classes and the timing of dispersion amongst regions.

NSG is a primary nursery area and source population for other regions. Variation in biomass was strongly related to three strong year classes that recruited in 1991, 1997 and 1999 and relatively poor recruitment throughout the 2000s. The population of SSG depends on migration from NSG. It was substantially replenished from the strong year classes in NSG during the 1990s, but its biomass subsequently declined through the 2000s due to low immigration. The West Coast also received input from the strong 1991 and 1997-year classes in NSG that had dispersed through SSG and then continued up the west coast of Eyre Peninsula. In the SE Region, the episodic fishery from 2008 to 2012 was related to the strong 2001 and 2004-year classes in Port Phillip Bay (PPB), Victoria. Some fish left the bay at around 3 – 4 years of age and moved hundreds of km westward, many reaching the SE Region. For SGSV, some fish from PPB moved even further west and eventually recruited to this region. Alternatively, fish from other year classes originated in either Spencer Gulf or the northern part of Gulf St. Vincent and subsequently moved into this region. Fish from different natal origins mixed in the waters of SGSV, which suggests that it is located at the boundary of different stocks. Through the 2000s, NGSV experienced a significant increase and then decline in biomass. It is likely that initially there was some input by immigration of the strong 1991 and 1997-year classes from NSG, relating to the general dispersion that occurred associated with these year classes. After this, the regional population of NGSV became self-sustaining, and generated a sequence of strong year classes that recruited between 2001 and 2009. Subsequently, the annual recruitment rates declined leading to the later reductions in biomass.

Keywords: Snapper (*Chrysophrys auratus*), life history, population biology, reproductive biology, egg development, larval development, recruitment variability, adult ageing, otolith chemistry, genomics, population connectivity and stock structure, acoustic telemetry, population dynamics.

PREAMBLE

One species of fish that has most instilled itself into the psyche of the Australian people is the Snapper (*Chrysophrys auratus*). This is a large, iconic, attractive, charismatic, long-lived, demersal finfish species. It has a broad distribution throughout the Indo-Pacific region that includes the temperate and sub-tropical waters of Australia (Kailola et al. 1993). This distribution includes the coastal waters of the southern two thirds of the Australian continent, southward from Shark Bay in Western Australia, along the southern continental coastline and up the east coast to Hinchinbrook Island in north Queensland (Kailola et al. 1993), as well as some coastal waters of Tasmania (Last et al. 2011). Throughout this unusually broad distribution, Snapper is a premium species that is recognised for the high quality of its flesh for human consumption. As each Australian mainland State supports important commercial, recreational and charter boat fisheries for Snapper, this species constitutes one of Australia's most significant fishery resources.

The coastal waters of the State of South Australia constitute the middle of the broad Australian distribution of Snapper. In this State, this species has been an important targeted fishery species at least since the early colonial days. For a number of years around the early 21st Century, South Australia produced the highest State-based commercial catches of Snapper, as well as high recreational catches (Fowler et al. 2013). This bonanza, however, did not last. From 2010, the State-based catches declined to their lowest levels since the early 1960s, reflecting reductions in catches and catch rates that related to significant declines in biomass. These were associated with changes in the spatial structure of the fishery as well as the fishing methodology used by commercial fishers. The reductions in fishery production led to changes in the stock status classifications that were assigned in stock assessments (Fowler et al. 2020, Drew et al. 2022). From 2010 onwards, the declining nature of the changes caused increasing levels of concern amongst fishers, fishery managers and scientists (Fowler et al. 2013, 2016, 2019). They led to a significant investment of scientific effort over the following decade, to consider the causes of the declines (Fowler et al. 2016). Also, throughout the decade, considerable management changes were implemented, to try to arrest the stock declines by limiting fishery catches and maximising opportunities for fish to spawn and for subsequent recruitment success (Fowler et al. 2020). Nevertheless, by 2019, it was apparent that the management changes had not arrested the declines, indicating the need for more drastic fishery management action (Fowler et al. 2019). In November 2019, the extraordinary action was taken to close the main South Australian Snapper fisheries. They were first closed until January 2023, but after it was apparent that the stocks had not recovered, the fishery closures were further extended until July 2026 (Drew et al. 2022).

It is important to understand the nature of the declines that the South Australian Snapper stocks experienced. Such understanding would provide insights into managing the closed fisheries towards recovery and after their re-opening. Furthermore, stock declines for Snapper have been occurring in other Australian jurisdictions (Fowler 2016), so any understanding for South Australia would likely be of broader interest and applicability. Whilst the intensity of scientific research has increased over the past decade, research into the life history and population biology of Snapper in this State has occurred for approximately 50 years, providing a wealth of knowledge, experience and understanding. However, the resulting literature and anecdotal information is disparate, which makes it difficult to access. The purpose of this report has been to collate, synthesise and summarise such information, including the anecdotal knowledge, to provide a comprehensive resource for this important jurisdictional fishery. The intended audience is the current and future researchers, to provide the most comprehensive and accessible information on the population biology of the species and from where it came. Parts of the report are also likely to be of interest to fishery managers, researchers in other jurisdictions, and fishing industry representatives.

During preparing this report, the intention has been to be inclusive with respect to retaining detail, rather than being selective and exclusive. Where possible, a chronological approach was adopted that described the methodological approaches, their outputs, and the development of understanding. It describes the empirical methodologies and summarises results from when fishery research on Snapper commenced in the late 1970s up until completion of the stock assessment in 2020 (Fowler et al. 2020), although occasionally some later results are also included. The report begins by describing the development and history of the South Australian Snapper fishery, whilst it is largely focussed on the descriptions and ecology of the different life history stages. The topics include: (1) the reproductive biology; (2) the development of the eggs and larvae and their spatial patterns of distribution and abundance; (3) the early life history and recruitment of juvenile fish and environmental influences; (4) adult biology based on ageing fish from their otoliths and describing movement patterns using acoustic telemetry; (5) the connectivity amongst populations and stock structure from otolith chemistry and genetic studies; (6) and the report concludes with a description of the demographic processes that occurred through the 1990s and 2000s that led to declines in stocks and downgrades in stock status that warranted the closure of the fisheries.

This report does not mark the completion of scientific work on Snapper in South Australia. Rather, following the extension of the fishery closures until 2026, the State Government and the Fisheries Research and Development Corporation (FRDC) have co-funded a significant science program and support package. This includes a National Snapper Science Program comprising three themes aimed at improving the understanding of the population biology and ecological requirements of the species (FRDC 2023/085 – Snapper Science Program: Theme 1 - Biology and Ecology), as well as improving the methods used for the collection of data that underpin and the processes involved in undertaking stock assessments (FRDC 2023/091 – Snapper Science Program: Theme 2 – Estimates of Biomass) that will culminate in the delivery of the next Snapper stock assessment report in late 2025 (Theme 3). This initiative is in addition to two current FRDC projects: FRDC 2019/044 – Quantifying post-release survival and movement of Snapper (*Chrysophrys auratus*):

informing strategies to engage the fishing community in practises to enhance the sustainability of an important multi-sector fishery; and FRDC 2019/046 – Cost-effective, non-destructive solutions to developing a pre-recruit index for Snapper.

1. HISTORY AND DYNAMICS OF SOUTH AUSTRALIA'S SNAPPER FISHERY

1.1 Introduction

At least since the colonial period in South Australia's history, the finfish species Snapper (*Chrysophrys auratus*) has been a significant fishery resource that has contributed to the sustenance of the local inhabitants. It has been a primary target species of commercial fishers for sale through domestic and inter-state markets. For the recreational sector, Snapper has been an iconic target species because of the propensity of such fishers to pursue large trophy fish. Throughout the early 2000s, South Australia was the dominant jurisdiction contributing to the national commercial catches, whilst also providing significant catches for the recreational sector (Fowler 2016, Fowler et al. 2020). Nevertheless, in November 2019, total fishing closures for both sectors were implemented for the two main fisheries located in South Australia's gulfs and west coast that prohibited the targeting and take of Snapper, including tag and release activities. The closures were the result of considerable declines in both fisheries and associated downgrades in the classification of stock statuses that had occurred throughout the previous decade (Fowler et al. 2019, 2020; Drew et al. 2022).

Prior to the fishery closures, South Australia's Snapper fisheries were geographically extensive, encompassing most of the State's coastal marine waters from the far west coast of Eyre Peninsula to the southeast region between the Coorong and the Victorian border, although catches were generally highest from the gulf region of Spencer Gulf, Gulf St. Vincent, and Investigator Strait (Fowler et al. 2016, 2019, 2020; Steer et al. 2018, 2020). Licence holders from four different commercial fisheries had access to the Snapper stocks. Most catch and effort had been accounted for by the Marine Scalefish Fishery, whilst relatively minor catches were reported by the Northern Zone and Southern Zone Rock Lobster Fisheries and the Lakes and Coorong Fishery (PIRSA 2013). The Marine Scalefish Fishery is the oldest and most complex fishery in South Australia, whose humble origins date back to the early colonial period (Wallace-Carter 1987). For numerous decades the fishery has been a multi-sector, multi-taxa, and multi-gear fishery for which the fishers had access to technologies that facilitated quick access to fishing grounds, navigation and finding the fish. For the heterogeneous commercial sector, prior to the fishery closures, Snapper was one of the four primary target species that accounted for a high proportion of the total effort as well as the volume and total production value of the catch (Smart et al. 2022).

The first chapter of this report considers the development of South Australia's Marine Scalefish Fishery, from its humble beginnings to the modern complex fishery of the 21st Century, particularly focussing on the Snapper fisheries, i.e., considering how the regional fisheries developed and changed over time, until it was ultimately necessary to close the fisheries. It is valuable to place a modern fishery in its historical context because of ‘shifting baselines’ that occur amongst different generations of fishers, fishery managers and scientists, as the perceptions of what are acceptable fishery catches, population sizes and characteristics can change over time (Pauly 1995). Developing some understanding of how populations of a fishery species may have changed through periods of history provides a broad temporal context in which to consider contemporary datasets (Saenz-Arroyo et al. 2006, Izzo et al. 2016). This is useful because recent population and fishery data may not adequately represent what they were like historically. Having such understanding allows fishery and natural resource managers to consider the unimpacted potential productivity of a fish species and its broader ecosystem when setting and prioritising management goals and developing appropriate targets for fishery management and future exploitation.

To take a historical consideration of a fishery and to recognise shifts in baselines, information from earlier time periods is required to reconstruct what populations were like (Izzo et al. 2016). For Snapper fisheries in other jurisdictions, such an historical approach has been useful in demonstrating significant anthropogenic influences on the sizes and characteristics of fish populations. A study for southeast Queensland produced the earliest known catch rate estimates for this species and demonstrated a considerable decline in catch rate between 1871-1939 and 1993-2002 that was indicative of a significant reduction in fishery productivity between the two periods (Thurstan et al. 2016). In New Zealand, where Snapper populations have been exploited for hundreds of years, historical and archaeological explorations have indicated significant changes in Snapper populations with respect to biomass, size and age structures and the behaviour of the fish (Leach and Davidson 2000, Parsons et al. 2009).

The general aim of this chapter was to consider the historical development of the Snapper fishery in South Australia. The purpose was to assess whether, based on historical information, it would be possible to infer how catches of Snapper are likely to have changed over time and to consider the possible impacts that fishing may have had on the populations in terms of their abundances, biomass, and characteristics. Official records of Snapper catches are available since 1951, although there are some data from the Adelaide market from 1936 onwards (Alleway et al. 2014). As such, there are some quantitative fishery data, but only for the recent part of the extensive period during which human extraction from them has occurred. For the period prior to the availability of official records, Snapper are mentioned in historical accounts of the developing fisheries (Wallace-Carter 1987), as well as in reports to Parliament. The question is whether such largely anecdotal accounts contain useful qualitative information that provide insights into the nature of the historic Snapper populations.

1.2 Materials and methods

The long-term history of fishing activity in South Australia and the development of the Marine Scalefish Fishery were described by Wallace-Carter (1987). This publication is the primary source for much of the historical descriptions that are provided here of the development through the colonial and post-colonial periods of the 19th and 20th Centuries.

1.2.1 Commercial fishery statistics

Over the past 70 years or so, some statistics have been recorded on an annual basis regarding the commercial sector of the Marine Scalefish Fishery, particularly the fishery catches. Several approaches for obtaining, recording, and reporting on such data were used during these periods that differed with respect to the sophistication of the data collected and their usefulness in a management context.

Prior to July 1983

Between 1964/65 and 1989/90, annual estimates of the commercial catches of Snapper were accessed from the Bureau of Rural Resources (BRR). Estimates of catches were provided in Working Paper No. WP/14/91 entitled ‘Twenty-Five Years of Australian Fisheries Production’. For prior to 1968, estimates of landings were collected directly from co-operatives and fish processors by the South Australian Department of Fisheries, which were then provided to the Australian Bureau of Statistics (ABS). From 1968, a system of monthly catch and effort returns was in operation in South Australia. From 1976 to July 1983, the ABS processed these catch returns and provided estimates of regional summaries to the South Australian Department of Fisheries via computer printouts. Through this period, the fishers provided only minimal data on their fishing effort, i.e., the number of days that were fished per month. As the Marine Scalefish Fishery is a multi-species fishery this precluded the possibility of differentiating the amount of effort that was targeted towards the different species, including Snapper, thereby preventing species-specific catch rates from being calculated. As such, estimates of commercial fishing effort and catch rate are not considered for this period.

For the period of 1951/52 to 1970/71, annual commercial production figures were compiled with the co-operation of commercial fish buyers and local inspectors. These were compiled as entries and recorded manually in a document entitled ‘SA Fisheries Production’.

July 1983 onwards

Since July 1983, it has been mandatory for South Australia's commercial Marine Scalefish fishers to submit a monthly catch return that provides details about their fishing activity in the preceding month. Such data include the species of fishes that were targeted, the fishing effort and gear types, the amounts of all species that were retained and the marine fishing areas where the fishing activity took place (Fowler et al. 2020). Up to June 2003, monthly totals for catch and effort could be reported, but since July 2003, reporting on daily fishing activities has been mandatory. For this report, the catch data for Snapper provided by individual fishers were accumulated to provide annual total catches for the calendar years from 1984 to 2019 for the regional populations that comprise the three stocks that occur in South Australian waters; Northern Spencer Gulf (NSG), Southern Spencer Gulf (SSG) and the West Coast of Eyre Peninsula (WC) for the Spencer Gulf/West Coast Stock; Northern Gulf St. Vincent (NGSV) and Southern Gulf St. Vincent (SGSV) for the Gulf St. Vincent Stock; and the population of the south east region of South Australia (SE Region) that is part of the Western Victorian Stock (Fig. 1.1). For each regional population, detailed analyses of the estimates of total annual catch, targeted gear-specific catches, effort and catch per unit effort (CPUE), and numbers of fishers are provided in Appendix 1.7.1.

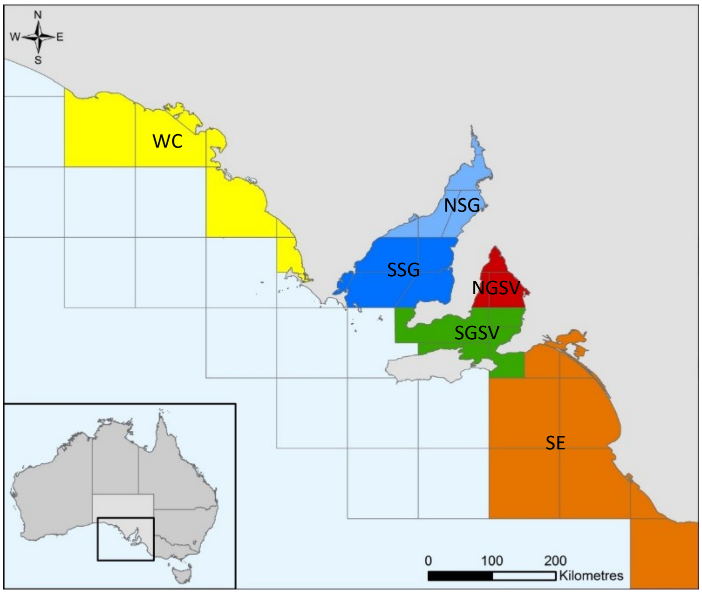


Fig. 1.1. Map of South Australia showing the division of coastal waters into six regions; NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – south east Region, WC – west coast of Eyre Peninsula. Grid lines indicate marine fishing areas.

1.2.2 Recreational fishery statistics

There have been four recreational fishing surveys undertaken in South Australia that have provided recreational catch and effort data for Snapper at both the regional and State-wide spatial scales. The first was a creel survey that was done across the years of 1994-96 that used the ‘bus-route’ method for surveying fishers at boat ramps (McGlennon and Kinloch 1997). The three subsequent surveys used the telephone/diary methodology and were done in 2000/01 (Henry and Lyle 2003, Jones and Doonan 2005), 2007/08 (Jones 2009), and 2013/14 (Giri and Hall 2015). The results from these surveys for Snapper are summarised in Fowler et al. (2007) and Fowler et al. (2016).

1.3 Results

1.3.1 Historical fishery information

Aboriginal fishing

For thousands of years prior to arrival of European settlers, the coastline of South Australia was inhabited by indigenous Aboriginal people for whom fish contributed to their diets and fishing to their food gathering activities (Bryars et al. 2008). Their fishing activities involved the use of spears, fish traps, nets and snares, and rush mat scoops (Santich 1998). They also used arrangements of rocks, nets, and sticks to trap fish at low tide. Nets were used by men who would wade or swim out to enclose schools of fish that were then drawn to the beach (Santich 1998). As distinct from tribes of Aboriginals who lived in other Australian regions, those in South Australia did not use lines and hooks in their fishing activities (Pepperell 2018). As such, based on their fishing techniques and gear, it appears that the fishing operations of the local Aboriginal fishers would likely have essentially been restricted to inter-tidal or shallow, sub-tidal, nearshore waters. It seems unlikely that these activities would have impacted strongly on the populations and demographic processes of sub-tidal marine species such as Snapper (Bryars et al. 2008). Although there are stories about the acres of water being pink with Snapper at spawning time, it is unlikely that the biomass or demographic processes of such populations were significantly impacted by the fishing of the Aboriginal people.

European Settlement – Colonial Period

During the very early 19th Century, the coastline of South Australia was explored by European marine expeditions such as those led by Captains Matthew Flinders and Nicolas Baudin (Thomas 2002). Also, around this time, early settlements were established on Kangaroo Island by whalers and sealers (Wallace-Carter 1987). It is likely that fishing contributed to the sustenance of the crews of these early expeditions and settlements, but there is little information available on the fish species caught or sizes of catches (Pepperell 2018). In 1836, under the guidance of Colonel William Light, the main European settlement was established at Adelaide on the eastern shore of Gulf St. Vincent. Fishing the waters of this gulf provided an immediate source of fresh food for the developing colony. At first, however this fishing was extremely limited in capacity as fishers deployed nets from dinghies that were rowed in the nearshore waters along the Adelaide coastline. Nevertheless, the fisheries quickly expanded along the eastern shore of Gulf St. Vincent and within a few years their geographic extent had extended northwards to Port Wakefield. Furthermore, fishers had started to use small sailing vessels, which allowed them to venture further offshore. By 1839, Snapper was recognised as one of a diversity of target species that were being taken in the fishery.

In South Australia, the geographic expansion of coastal fishing occurred relatively quickly. During the 1840s and 1850s, numerous townships were developed around the coastlines of Gulf St. Vincent, Spencer Gulf and in the SE Region. For each township, it is likely that a local fishery was quickly established to provide fresh food to the local inhabitants whilst other means of food production were developed.

In the latter 19th Century, the geographic expansion of fishing in the marine waters of South Australia continued as some fishers from Adelaide began using ‘cutters’ as fishing vessels. These were relatively large, seaworthy craft which provided a steady platform from which several fishers could operate. They contained live-wells into which the line-caught fish were placed to keep them alive. Such vessels could spend several days at sea before they had to return to port to off-load their catches. This allowed the geographic range of the fishing operations to increase considerably. Multi-day fishing trips were made to Investigator Strait, Backstairs Passage, and the southern parts of both gulfs. The two primary target species of these fishing operations were Snapper and King George whiting (KGW) (*Sillaginodes punctatus*). In the first instance, the cutter fishers were English and Scottish. However, the diversity of fishers increased through this period with the arrival of Scandinavian, Greek and Italian fishers who brought their own fishing methodologies with them.

In the first instance, the cutters had to return to Adelaide to off-load their catches. This would have impacted on their ‘effective effort’, as fishing time was reduced by sailing to and from the fishing grounds. However, towards the end of the 19th Century alternative means of transporting catches to Adelaide and other destinations were developing. Steamers began to trade around Gulf St. Vincent, Spencer Gulf, and the SE Region for the transport of passengers and produce. Also, from the 1860s to the 1890s, the rail line was built from Adelaide to Port Wakefield in northern Gulf St. Vincent and then eventually across to the towns in northern Spencer Gulf such as Wallaroo and Moonta. This meant that fishery catches could be transported by rail from the towns of both northern gulfs to Adelaide, Melbourne, and Broken Hill.

Changing to the 20th Century

Towards the end of the 19th Century, the fishing industry in South Australia was well-established and was geographically extensive throughout the coastal waters of both gulfs, Investigator Strait, Backstairs Passage, and the SE Region. The fishing fleet in Adelaide involved sailing vessels that ranged from small boats that were operated daily to an increasing number of larger cutters that engaged in multi-day trips. The smaller vessels were used in the northern gulf to seine-net smaller species and in the southern gulf between Glenelg and Cape Jervis to target Snapper and KGW. In Gulf St. Vincent, the cutters were based in Glenelg, and were used to fish for Snapper and KGW in Investigator Strait, Backstairs Passage and along the north coast of Kangaroo Island. Between 1884 and 1910, the numbers of cutters that operated from Glenelg increased from four to 34, becoming the backbone of the fishing industry. Snapper was consistently recognised as one of the primary species of the line fishers who operated broadly throughout the coastal waters of South Australia, although their catches were more variable than the more consistent ones of KGW (Wallace-Carter 1987).

By the 1870s, concerns were emerging in South Australia about the status of the fished stocks. In response, in 1878, the first State Fisheries Act was developed for the protection and preservation of fish. Also, the first Inspector of Fisheries was appointed, i.e., the first step towards enforcing new regulations. The Act was the precursor to a suite of further regulations that were introduced to maintain the focus on protecting fish stocks. These included: in 1888, the introduction of minimum legal weights for the different fish species; and in 1904, the introduction of licencing for commercial fishers. In 1917, these various fishery acts were consolidated into one which: required that commercial fishers be licensed, and their boats be registered; used minimum legal weights for the different fish species; introduced limits to nets and other gears; and used closed seasons and closed areas as fishery management strategies.

Throughout the 20th Century, the changes in the Marine Scalefish Fishery related to developments in technology that facilitated the catching of fish and their preservation during transportation and marketing. The numbers of commercial fishers varied considerably over time, relating to social and economic pressures associated with domestic and world events. When commercial fishing licences were first introduced in 1905, there were 476 commercial fishers. This number increased quickly to 1,400 in 1914, but then fell to 800 during WWI as many fishers left the industry to enlist for military service. Then, during the 1930s, the numbers again increased due to the Great Depression, reaching 1,463 in 1934.

From WWI onwards, there was the gradual introduction of using motors in boats, although the change-over from wind power was slow. It took until the 1970s before many of the old cutters were replaced with faster vessels with planing hulls. The use of powerful engines with line-fishing boats allowed fishing operations to be carried out in a single day rather than requiring multi-day trips. There were also important advancements in fish preservation during the 20th Century. Through the history of the fishery, getting the fish to market in good condition had been problematic and largely weather-dependent, given the need for fish catches to be transported over long distances from regional areas by steamship to Adelaide, and by rail to Melbourne and Broken Hill (Wallace-Carter 1987). It wasn't until the 1930s that the large-scale production of ice at many fish ports and utilisation of refrigeration largely circumvented the transport problems.

During the 1960s and early 1970s there were substantial increases in numbers of commercial fishers as well as the equipment and technology available to them. During the 1960s, the fishing industry was impacted by a technical revolution, which resulted in an influx of labour. This related to the displacement of personnel from the agricultural sector due to mechanisation. The increase in numbers of participants in the fisheries in the gulfs and west coast bays up to 1,771 licenced commercial Marine Scalefish Fishers by 1972, resulted in a substantial increase in fishing effort. Furthermore, during the 1970s, there was considerable advancement in the technology of boats and fishing gear, as well as the introduction of 'sounders' on fishing vessels, i.e., early acoustic devices for detecting fish and the seafloor.

The changes in numbers of personnel and the technical advancements through the 1960s and 1970s resulted in substantial increase in fishing effort and efficiency. This prompted the need for a change to fishery management that was based around controlling and reducing fishing effort. In November 1972, the Marine Scalefish Fishery was made a limited-entry fishery, with the number of licence holders capped at 1,771. Subsequently, the principal strategy became to reduce the numbers of fishers in the commercial sector (Kumar and Hill 1999). First, in 1979, licences were not re-issued if a minimum level of fishing had not been achieved. Then, in 1994, a licence amalgamation scheme was introduced, whereby any new entrant to the fishery could only do so by purchasing two existing licences (Steer and Besley 2016). This aimed to decrease fishing effort by reducing the numbers of participants and to remove latent effort from the fishery. The strategy proved highly successful as between 1984 and 2014 there was a 57.4% reduction in numbers of Marine Scalefish licence holders from 666 to 284, and a 52% reduction in fishing effort.

Throughout the 1980s and 1990s, electronic navigation equipment such as satellite navigation, GPS and radar were incorporated onto the vessels, as well as fish finding devices such as echo sounders and sonar (Jones and Luscombe 1993a,b). Such developments further increased the fishing power of the individual licence holders. Since the 1990s, fishing technology has continued to advance through the development of light-weight gear, automatic winches and reels, radar and 3D bathymetric imaging (Steer et al. 2014).

1.3.2 Commercial fishery catches

State-wide catches from 1951/52 to 2019/20

Official records of Snapper catches at the State-wide scale are available back to 1951. For the period of 1939/40 to 1946/47, there are annual estimates available for the weights of Snapper that passed through the Adelaide Fish Market. These ranged from 23 to 60 $t.yr^{-1}$, but such estimates are likely to have been lower than the State-wide catches as they would have excluded all catches from regional areas and those sent inter-state.

Since 1951/52, there has been a general increase in the commercial catches of Snapper, although they displayed some cyclicity, increasing and decreasing over periods of several years (Fig. 1.2). There were four periods in the time-series of estimates of annual commercial catches. From 1951/52 to 1972/73, the catches increased relatively consistently from <200 to >500 t.yr^{-1}. Then, in 1974/75, the annual catch declined quickly and from then until 1994/95 there was no obvious long-term trend. From 1974/75 until 1982/83 the catches ranged from 300 to 400 t.yr^{-1}, whilst from 1983/84 until 1992/93 they were generally >400 t.yr^{-1}. Over the next two years, they dropped considerably to the low level in 1994/95 of 223 t, the lowest estimate of catch since 1959/60. The catches had declined from 1991/92 to the long-term minimum in 1994/95 before having increased quickly up to a high level in 2001/02. After a further decline until 2003/04, there was a period of substantial increase up to the historic maximum catch in 2010/11. Subsequently, the annual catches declined considerably to 281 t in 2018/19, the lowest since 1994/95 and second lowest since 1963/64. The presented catch for 2019/20 was only to November 2019, when the fisheries for the Gulf St. Vincent and Spencer Gulf/West Coast Stocks were closed to fishing.

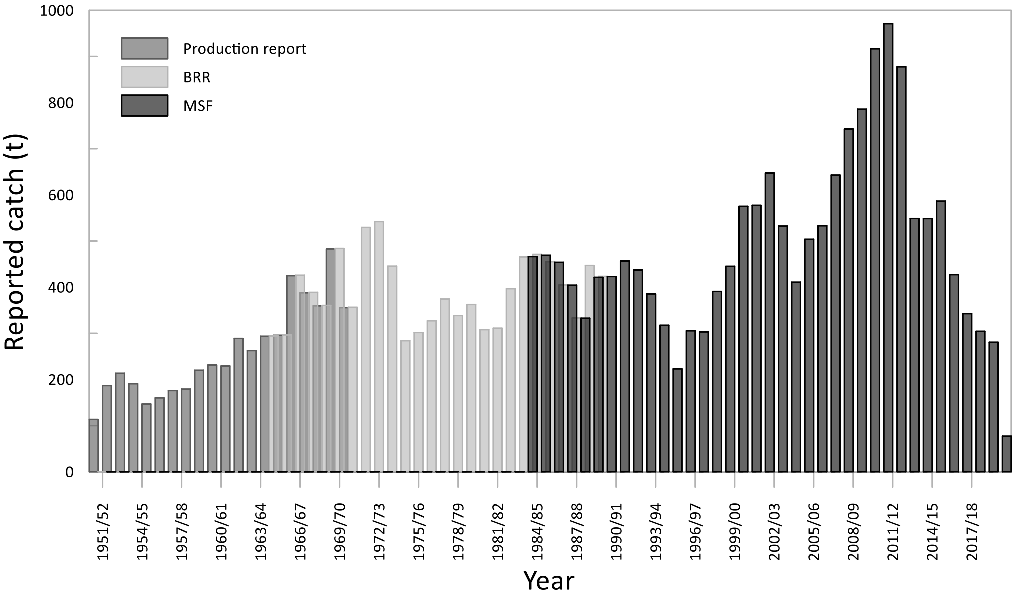


Fig. 1.2. Estimates of total annual commercial catches of Snapper for South Australia from 1951/52 to 2019/20. The estimates for different time periods come from three different sources (refer Materials and Methods). The two periods of overlap between the three datasets are evident. Abbreviations: BRR – Bureau of Rural Resources; MSF – Marine Scalefish Fishery.

There were two periods of overlap between the three datasets, i.e., between the production figures and those in the BRR report for 1964/65 to 1970/71; for the period of 1983/84 to 1989/90 between the BRR report and the Marine Scalefish Fishery Information System. In both cases, the overlapping data from the two sources were similar, suggesting that they had most likely originated from the same source or same methodology. This consistency in estimates provides some confidence that the correct figures were being considered for the different periods.

1984 to 2019

The current comprehensive system of reporting by commercial fishers was implemented in July 1983, allowing for a higher level of resolution in fishery statistics. Estimates of total commercial catch are considered here in detail by calendar year. Since 1984, the cyclicity in State-wide commercial catches of Snapper has been most pronounced (Fig. 1.3a). Three cycles are apparent that reflect near-decadal modes in annual catches, i.e., with peaks in 1990, 2001 and then 2010. For the most recent mode, the catches increased from 412 t in 2003, to the record catch of 1,035 t in 2010 before declining to 2019, when the 2nd lowest catch of 252 t was recorded.

From 1984 to 2004, most of the commercial catches of Snapper were taken with handlines, with longlines as the second most significant gear type (Fig. 1.3a). However, the considerable increase in catch that occurred through the 2000s, was associated with a significant shift in methodology from handline to longline fishing, as fishers adopted new efficient longline technologies. The early success of the new longline approaches attracted more fishers to target Snapper which resulted in further increases in targeted fishing effort (Appendix 1.7.1, Fig. A1.4). Consequently, the relative proportions of annual State-wide catches taken with longlines increased from 2004 onwards and by 2010 they accounted for the higher proportions of these total catches (Fig. 1.3a). The dominance of longline fishing remained until the fishery closures in 2019.

Concomitant with the gear changes described above, there was a dramatic change in the spatial structure of South Australia's fishery. Prior to 2003, the relatively small region of NSG (Fig. 1.1) had generally contributed >50% of the State's catch of Snapper (Fig. 1.3b). However, from 1999 onwards, the catches from this region declined, whilst those from SSG increased. From 2005 to 2009, SSG dominated the catches from Spencer Gulf and were also the highest regional catches across the State. However, from 2007 onwards particularly in 2012, the catches from SSG declined. After this, only low catches were taken in SSG and NSG. Nevertheless, as the catches from these two regions were declining, there were exponential increases in those from several other regions, notably NGSV and the SE Region, and most recently from SGSV (Fig. 1.3b). From 2009 to 2012, NGSV and the SE Region largely accounted for the record State-wide catches taken through this period. Those from the SE Region were particularly high in 2009, 2010 and 2011 before falling in 2012 and 2013. Between 2010 and 2016, the catches from NGSV made the highest contribution to the State-wide catches, before they also declined between 2016 and 2019. In 2019, for the first time, SGSV produced the highest catch of the six regions. These data indicate that the regional fishery that made the most significant contribution to the State-wide catches changed over time. Initially, NSG was the most significant contributor, which then gave way to SSG. Then, as the catches from these two regions declined, those from NGSV and the SE Region increased to record levels. Then, the catches from these two declined, and by the time the fishery closures were imposed in 2019, SGSV was the region that was producing the highest catch.

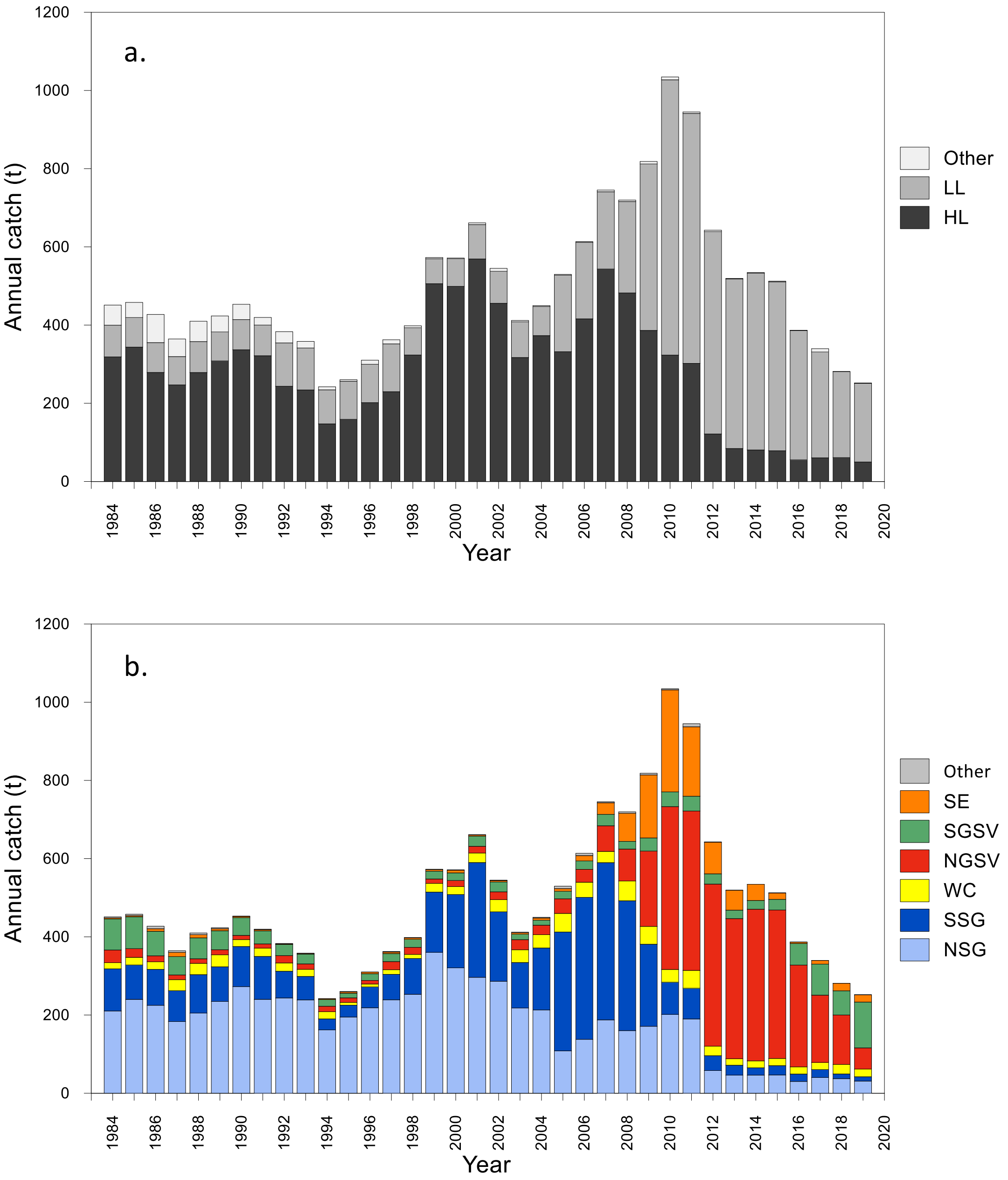


Fig. 1.3. State-wide annual commercial catches of Snapper from South Australia. a. annual commercial catches by the main gear types. b. annual commercial catches by region.

1.3.3 Development of the recreational sector

The development of the recreational sector of the Marine Scalefish Fishery has been less well chronicled than the commercial sector. Whilst some anecdotal descriptions are available, there is only limited information from recent decades. It is apparent from anecdotal descriptions from one family's fishing activities that at least by the late 1940s, recreational boat fishers operated in South Australia's nearshore coastal waters, targeting Snapper and producing relatively good catches and catch rates (Hawes 2016). Nevertheless, it is likely that, recreational catches through the 1940s, 1950s and 1960s were limited compared to those taken in later years because of the lower human population size and the limited technology available. The recreational fishing operations at that time, as described, were very simple (Hawes 2016). On the western side of Gulf St. Vincent there was limited access to bays by road, as well as a lack of accommodation, facilities, and infrastructure. The fishing was done from small boats with low-powered outboard motors, which limited the range of travel. Navigating and finding fishing spots were done using visual marks of features on the land. The anecdotal descriptions reported few encounters with other boat fishers, either commercial or recreational, suggesting that fishing effort in Gulf St. Vincent at that time was relatively low (Hawes 2016). It is likely that recreational fishing effort increased through the 1970s and 1980s as the human population increased and social reforms led to lower working hours providing fishers with more leisure time (Wallace-Carter 1987). Also, the improvements in boating and fishing technology that were adopted by commercial fishers were also available to the recreational sector. By 1987, there were 40,000 recreational boats registered in South Australia, which would have included many fishing boats. By the late 1970s or early 1980s, recreational fishing had developed to the extent that the South Australian Recreational Fishing Advisory Committee was formed to co-ordinate recreational fishing groups and to participate in the fishery management process (Wallace-Carter 1987). Another anecdotal account, this time from a commercial fisher who, based on a lifetime of fishing in NSG, pointed out the significant increase in the numbers of recreational fishing vessels that occurred between the 1960s and the late 1980s and the significant increase in their technological advancements (Simms 1988).

The four State-wide recreational surveys that were done through the 1990s and 2000s provided important indications of the extent to which the recreational sector had developed in South Australia (McGlennon and Kinloch 1997, Henry and Lyle 2003, Jones and Doonan 2005, Jones 2009, Giri and Hall 2015). By the 2000s, estimated participation rates included many thousands of fishers who engaged in millions of recreational fishing events per year and caught millions of fish. In 2013/14, i.e., the most recent survey during which the Snapper fisheries were still open, there was an estimated total of 4.9 million finfish retained by recreational fishers that included an estimated 207,809 Snapper with an estimated harvest of 332.5 t (Fig. 1.4). This was less than the recreational harvest of 416 t in 2000/01 but was higher than that of 178 t in 2007/08.

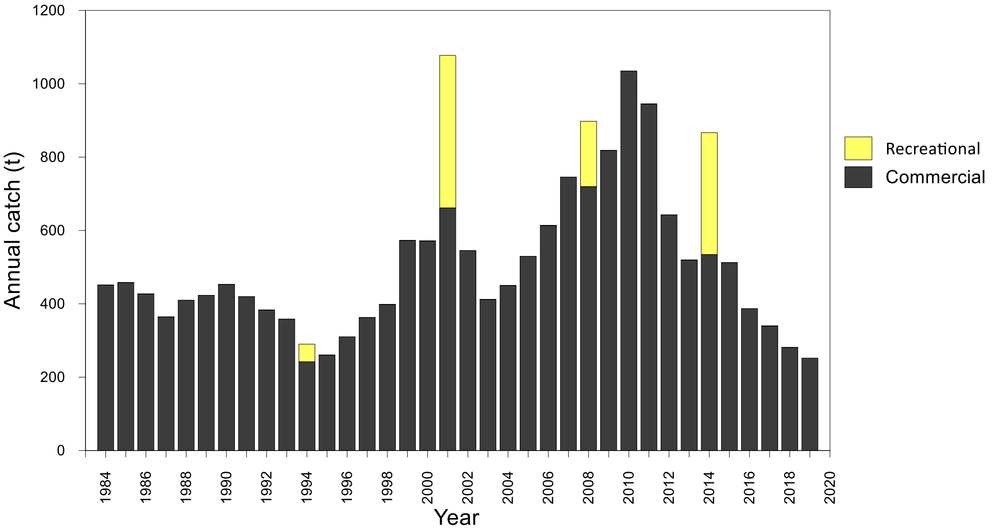


Fig. 1.4. Estimates of annual State-wide commercial catches of Snapper between 1984 and 2019 as well as the estimates of recreational catches of Snapper from four State-wide recreational fishery surveys.

1.4 Discussion

1.4.1 Catches of Snapper

The historical development of fishing in South Australia was described here to explore likely trends in fishery catches of Snapper and to consider potential impacts of fishing on the populations. For the commercial and recreational fishery sectors, official estimates of Snapper catches are only available for relatively small proportions of the total period throughout which human extraction from these populations has occurred. For the commercial sector, records of catches are available for the past 70 years or so, whilst there are only four estimates of State-wide recreational catches, all recorded in the past 30 years. As such, the trends in catches during the early years of the fishery can only be estimated, based on qualitative descriptions of the development of the fishery throughout the different historical periods.

Prior to European exploration and settlement, the coastal fringes of South Australia were occupied for thousands of years by populations of indigenous Aborigines (Bryars et al. 2008). Given the fishing practices that these fishers engaged in, their activities would have largely been restricted to the very nearshore. Since Snapper primarily occupy deeper, sub-tidal habitats, it is very unlikely that the catches were sufficient to have impacted on the sizes or demography of the fish populations. This contrasts with the impacts of Snapper fishing by the Māori inhabitants in New Zealand between their arrival in 1280AD and that of the Europeans during the 19th Century. In the Hauraki Gulf in northern New Zealand, the Māori harvested thousands of Snapper annually (Parsons et al. 2009). It is now evident that the fishing activities of the early indigenous fishers were of a scale that caused changes in the biomass, size and age structures of the local New Zealand Snapper populations and the behaviour of the fish (Leach and Davidson 2000, Parsons et al. 2009).

For South Australia, European exploration of the coastline and the first basic settlements were established during the early 1800s. The early fishing activities, which involved deploying seine nets or fishing lines from small dinghies, were extremely modest and restricted to the nearshore (Wallace-Carter 1987). In the years following the establishment of the first permanent colonial settlement at Adelaide in 1836, there was significant geographic expansion as other townships were established around the South Australian coastline. The requirement to feed these communities, underpinned the expansion of the fishery into regional waters. Associated with this geographic expansion, between 1836 and 1900 the human population of South Australia increased from a few hundred individuals up to approximately 362,000 people (Fig. 1.5). As such, the numbers of fishers that operated in the State's waters must have increased considerably to help feed this expanding population. This would have been assisted by increases in fishing capacity that occurred during the 19th Century. With the use of cutters as fishing vessels, the duration of fishing trips increased, which allowed expansion to the southern gulfs, Backstairs Passage, and Investigator Strait. Furthermore, during the 1860s to 1880s, the diversity and capacity of the fishery increased with the arrival of experienced fishers from several European countries, who brought with them different fishing gear and techniques. Overall, during the 19th Century, fishing in South Australia was characterised by significant areal expansion, and associated increase in fisher numbers and capability. From the outset, Snapper was recognised as one of 'a diverse array of 'excellent' finfish species that were available in high abundances' (Wallace-Carter 1987). As it continued to be a primary target species, it is most likely that the fishery catches increased, perhaps at least in proportion with the increasing population and its requirement for food.

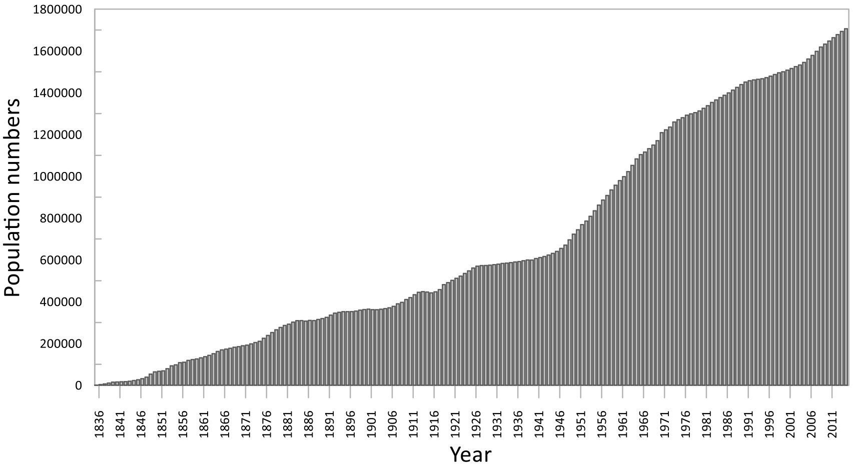


Fig. 1.5. Estimates of human population size in South Australia between 1836 and 2015 from The Australian Bureau of Statistics.

Throughout the 20th Century, the human population of South Australia continued to increase, particularly after World War II, as the number reached around 1 million in the early 1960s and approached 1.5 million during the 1990s (Fig. 1.5). Also, throughout this century, the numbers of commercial fishers increased along with the fishing technology. After licensing became mandatory in 1904, the numbers of commercial fishers were variable, reflecting events such as world wars and The Great Depression, but increased over the long-term from 476 in 1904 to 1,771 in 1972. Such variation in fisher numbers must have impacted considerably on fishery catches. Nevertheless, throughout the first half of the century fishing capacity largely remained limited as most fishing vessels still relied on wind power. As such, it is difficult to consider that the Snapper catches exceeded 200 $t.yr^{-1}$, which was approximately the total estimated annual catch during the early 1950s. However, from then until the late 1980s, the mechanisation and modernisation of fishing increased substantially, ultimately resulting in a modern fishing fleet of fast, planing-hull vessels that were equipped with sophisticated electronic equipment. Over this period, the annual estimates of commercial catches of Snapper more than doubled from <200 $t.yr^{-1}$ to >400 $t.yr^{-1}$. Furthermore, by the 1980s, the recreational sector had also become well established, reflected in the proliferation of recreational fishing boats that were used throughout the State's coastal waters (Simms 1988).

During the 21st Century, commercial and recreational fishers had access to fast, powerful boats, modern electronic equipment for navigating and finding fish, as well as strong, light gear for catching the fish. Through these years, the commercial catches of Snapper increased first to >600 $t.yr^{-1}$, and then to >1,000 $t.yr^{-1}$ around 2010. Also, during the 2000s, the estimated recreational catches were in the order of several hundred $t.yr^{-1}$. As such, it is likely that in some years around this time, the total State-wide catches of Snapper were close to 1,500 $t.yr^{-1}$. Nevertheless, from 2010 to 2019, the commercial catches declined considerably. It is likely that the recreational catches also declined through this period. So, it is most likely that the period between 2000 and 2011 was when the greatest human extraction from South Australia's Snapper populations occurred. In the recent stock assessments, the time series of annual fishery catches from 1984 to 2019 were considered with other demographic information using the 'SnapEst' computer fishery model (Fowler et al. 2020, Drew et al. 2022). The model outputs indicated that the reductions in fishery catches throughout the latter 2000s, related to significant declines in biomass of the Snapper populations from 2005 in Spencer Gulf and from 2011 in Gulf St. Vincent (Chapter 12, Fowler et al. 2020, Drew et al. 2022).

Prior to the closures of South Australia's Snapper fisheries in 2019, the populations had likely been fished for thousands of years. Between European colonisation approximately 200 years ago and the mid-2000s, the annual State-wide catches of Snapper increased from, at most, a few $t.yr^{-1}$ to approximately 1,500 $t.yr^{-1}$. Through this period there was extraordinary development in the technology available to both commercial and recreational fishers that greatly enhanced their capacities to travel, and to find and catch Snapper. Also, throughout this period, the number of people who fished for Snapper would have increased considerably, partly reflecting the increase in population size around the coastline. The numbers of commercial fishers are likely to have increased throughout both the 19th and 20th Centuries, but from the 1990s began to decline due to the licence amalgamation scheme (Steer and Besley 2016). Yet, based on the three State-wide recreational fishing surveys that were undertaken through the 2000s, it is apparent that the recreational fishing sector had developed to an extent that, on an annual basis, many thousands of fishers engaged in millions of fishing events, producing catches of millions of finfish that included hundreds of thousands of Snapper equating to hundreds of tonnes (Giri and Hall 2015).

1.4.2 Assessment of effects of fishing on Snapper populations

Prior to the 1980s there is a paucity of comprehensive statistical fishery data for South Australia’s Marine Scalefish Fishery. For Snapper, there is only limited information on State-wide catches back to 1951. This means that there is extremely limited capacity to consider the long-term impacts of fishing on populations. It is tempting to suggest that the biomass of the populations of Snapper would have declined throughout the 19th and 20th Centuries as a result of fishing that removed tonnes of fish per year from the populations, as would be expected for such a large, long-lived demersal species (Pauly et al. 1998, Ransom and Worm 2006, Izzo et al. 2016). For the Snapper fisheries, there are some limited anecdotal reports that support this notion. It is apparent that by the 1870s there were some marine fish stocks in South Australia that had been impacted by fishing through the preceding 40 years of the colonial period, which had led to the need for the first Fishery Act in 1878 (Wallace-Carter 1987). As Snapper was one of the primary target species of both the smaller, inshore fishers and those who used the larger cutters, it is likely to have been one of the impacted fish species. By the early 20th Century, some references indicated concern for Snapper populations. At that time, annual reports to South Australia’s State Parliament regarding the status of fisheries indicated that the Snapper fisheries were ‘less productive’ relative to earlier years (Duffield 1909, 1910, 1912, McIntosh 1915). This was evident in the ‘failure’ of the Snapper fishery in Investigator Strait in 1908, as well as the decline in reliability of Snapper in the southeast region that occurred after World War I (Wallace-Carter 1987). In 1921, it was reported in the Adelaide Advertiser that a proposal for introduction of a closed season between 1st December and 31st January for Snapper fishing was being put before the South Australian Parliament, because of a ‘great falling off in the supply in the past few years’. For later in the 20th Century, there is a significant anecdotal reference that points to the decline in the Snapper population of NSG. In 1988, a highly experienced commercial fisher who had spent his extensive working life fishing in NSG, having followed several generations of fishers in his family, lamented the decline in Snapper catches throughout this region, particularly around Moonta Bay. He claims that this decline was at least partly attributable to the proliferation in recreational fishing effort and the enhanced capacity of this sector (Simms 1988).

The anecdotal accounts presented above suggest that in the latter 19th and through the 20th Centuries there were downturns in some South Australian regional Snapper fisheries. The question is whether these downturns were indicators of reductions in biomass because of fishing, as has commonly occurred for Snapper in other jurisdictions and for many other species of fish with life-history characteristics like Snapper. In south-east Queensland, for Snapper there was an order of magnitude reduction in catch rate between the periods of 1871-1939 and 1993-2002 indicative of a substantial reduction in biomass (Thurstan et al. 2016), whilst the Hauraki Gulf in New Zealand experienced an estimated 80% reduction in Snapper biomass because of fishing (Izzo et al. 2016). The question can now be considered for Snapper in South Australia, in the light of our understanding of its population biology from the research undertaken over the past 50 years, as summarised in the following chapters of this report. The outcome is that we should be cautious about answering that question in the affirmative. It is now evident that in south-eastern Australia, Snapper populations experience considerable inter-annual variation in recruitment that drives the natural dynamics in abundances, biomass and size and age structures (Chapters 6, 9, 12). Even as recently as during the 2000s, it is evident that the South Australian regional populations demonstrated significant dynamisms in fishery production that reflected inter-annual variation in recruitment (Fowler et al. 2020). Consequently, with respect to the apparent downturns during the late 19th and through the 20th Centuries, there is insufficient information available to indicate whether they reflected periods of poor recruitment, the effects of fishing or a combination of both factors.

Despite uncertainty about the effects of fishing on the South Australian Snapper populations during earlier periods, during the first decade or so of the 2000s the highest catches recorded are likely to have contributed to the significant declines in biomass that became evident during the latter 2000s (Chapter 12, Fowler et al. 2020, Drew et al. 2022). However, understanding how these declines were manifested cannot be gleaned only from fishery information. Rather, such understanding must be based on a detailed understanding of the life history, population biology, demography, and stock structure of the Snapper populations. The following chapters provide chronologies and summaries of the findings of research on the population biology of Snapper in South Australia since the late 1970s. They inform our understanding of stock dynamics, including the recent declines that led to the need to close their fisheries. In so doing, this provides insights with respect to their assessment and management towards recovery, and subsequent future assessment and management.

1.5 References

Alleway, H.K., Connell, S.D., Ward, T.M., Gillanders, B.M. (2014). Historical changes in mean trophic level of southern Australian fisheries. Marine and Freshwater Research 65: 884-893.

Bertram A, Fairclough D, Sandoval-Castillo J, Brauer C, Fowler A, Wellenreuther M, Beheregaray LB (2022). Fisheries genomics of Snapper (*Chrysophrys auratus*) along the west Australian coast. Evolutionary Applications 2022: 15(7): 1099 DOI:10.1111/eva.13439.

Bryars, S., Harbison, P., Shepherd, S.A (2008). Historical background and present setting. In: Shepherd, S.A., Bryars, S., Kirkegaard, I., Harbison, P., and Jennings, J.T. (eds). Natural history of Gulf St. Vincent. Royal Society of South Australia Inc. pp 1-12.

Drew, M.J., Fowler, A.J., McGarvey, R., Feenstra, J., Bailleul, F., Matthews, D., Matthews, J.M., Earl, J., Rogers, T.A., Rogers, P.J., Tsolos, A., Smart, J.J. (2021). Assessment of the South Australian Marine Scalefish Fishery in 2019. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2017/000427-4. SARDI Research Report Series No. 1049. 259 pp.

Drew, M.J., Rogers, T.A., McGarvey, R., Feenstra, J., Matthews, D., Matthews, J., Earl, J., Smart, J., Noell, C., and Fowler, A.J. (2022). Snapper (*Chrysophrys auratus*) Stock Assessment Report 2022. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2007/000523-7. SARDI Research Report Series No. 1155. 178 pp.

Duffield, T. (1909). Report under the Fisheries Act for the period ending June 30th 1909. Adelaide, Australia.: House of Assembly.

Duffield, T. (1910). Report under Fisheries Act for year 1909-10. Adelaide, Australia.: House of Assembly.

Duffield, T. (1912). Report of Chief Inspector of Fisheries for year ended June 30th 1912. Adelaide, Australia: House of Assembly.

Fowler, A.J. (2016). The influence of fish movement on regional fishery production and stock structure for South Australia's snapper (*Chrysophrys auratus*) fishery. Final report to FRDC (Project No. 2012/020). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 181 pp.

Fowler, A.J., McGarvey, R., Feenstra, J.E., Jackson, W.B., Jennings, P.R. (2005). Snapper (*Pagrus auratus*) Fishery. Fishery Assessment Report to PIRSA for the Marine Scalefish Fishery Management Committee. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, RD03/0068-2.

Fowler, A.J., McGarvey, R., Feenstra, J.E., Jackson, W.B. (2007). Snapper (*Pagrus auratus*) Fishery. Fishery Assessment Report to PIRSA. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-1, SARDI Research Report Series No. 224. Pp 90.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E. Jackson, W.B. (2010). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-2, SARDI Research Report Series No. 473. Pp 109.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E., Jackson, W.B., Lloyd, M. (2013). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-3, SARDI Research Report Series No. 713. 103pp.

Fowler, A.J., McGarvey. R., Carroll, J., Feenstra, J.E., Jackson, W.B., Lloyd, M.T. (2016). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-4. SARDI Research Report Series No. 930. 82pp.

Fowler, A.J. Hamer, P.J., Kemp, J. (2017). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely-dispersed, coastal fishery species. Fisheries Research 189: 77-94.

Fowler AJ, Steer MA, McGarvey R, Smart J (2019). Snapper (*Chrysophrys auratus*) Fishery. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2019/000331-1. SARDI Research Report Series No. 1031.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111 pp.

Fowler, A.J., Stewart, J., Victorian Fisheries Authority, Roelofs, A., Garland, A., Jackson, G. (2021). Snapper *Chrysophrys auratus*. In Piddocke, T., Ashby, C., Hartmann, K., Hesp, A., Hone, P., Klemke, J., Mayfield, S., Roelofs, A., Saunders, T., Stewart, J., Wise, B., Woodhams, J. (eds). Status of Australian fish stocks reports 2020. Fisheries Research and Development Corporation, Canberra.

Gardner, M.J., Chaplin, J.A., Fairclough, D.V., Potter, I.C. (2022). Microsatellite-based assessment of the genetic structure of Snapper, *Chrysophrys auratus*, in Australasia. Estuarine, Coastal and Shelf Science. Doi: https://doi.org/10.1016/j.ecss.2022.107932.

Giri K, Hall K (2015). South Australian Recreational Fishing Survey. Fisheries Victoria Internal Report Series No. 62.

Godfriaux, B.L. (1974). Food of Snapper in Western Bay of Plenty, New Zealand. New Zealand Journal of Marine and Freshwater Research 8: 473-504.

Gomon M, Bray D, Kuiter R (2008). Fishes of Australia's Southern Coast. Museum Victoria. New Holland Publishers Pty Ltd, Sydney, Australia.

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Hawes, R.K. (2016). When Pop took us fishing. Sunshine Press. Australia. pp 167.

Henry GW, Lyle JM (2003). The national recreational and indigenous fishing survey. FRDC project 99/158, Final Report.

Izzo, C., Doubleday, Z.A., Grammar, G.L., Gilmore, K.L., Alleway, H.K., Barnes, T.C., Disspain, M.C.F., Giraldo, A.J., Mazloumi, N., Gillanders, B.M. (2016). Fish as proxies of ecological and environmental change. Reviews in Fish Biology and Fisheries 26(1): 265-286.

Jones K (2009). South Australian Recreational Fishing Survey. PIRSA Fisheries, Adelaide, 84 pp. South Australian Fisheries Management Series Paper No. 54.

Jones, G.K., Luscombe, M. (1993a). Fish and silicone chips. Quantification of technological changes in the Marine Scalefish Fishery. SAFISH 17(3): 6-7.

Jones, G.K. Luscombe, M. (1993b). Fish detecting devices. The impact of increasingly efficient navigational and fish detecting devices on the handline fishery for Snapper (*Pagrus auratus*) and King George whiting (*Sillaginodes punctata*) in South Australian waters. SAFISH 17(4): 9-13.

Jones K, Doonan A (2005). 2000-01 National recreational and indigenous fishing survey. South Australian regional information. South Australian Fisheries Management Series. Paper No. 46.

Kailola, P., Williams, M.J., Stewart, P.C., Reichlet, R.E., McNee. A., Grieve. C. (1993). Australian fisheries resources. Bureau of Resource Sciences and Fisheries Research and Development Corporation, Canberra.

Kumar, M.S., Hill, R. (1999). Impact of fishing regulations and policy of a multi-species fishery with respect to net and line fishing on the status of King George whiting (*Sillaginodes punctata*) stock in South Australia – a review. The Fourth Indian Fisheries Forum Proceedings (24-28th November 1996). Pg 361-365.

Last, P.R., White, W.T., Glehill, D.C., Hobday, A.J., Brown, R., Edgar, G.J., Pecl, G. (2011). Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practises. Global Ecology and Biogeography 20: 58-72.

Leach, F., Davidson, J. (2000). Pre-European catches of Snapper (*Pagrus auratus*) in northern New Zealand. Journal of Archaeological Science 27: 509-522.

Lloyd, M.T. (2010). Spatial variation in growth of snapper (*Chrysophrys auratus*) in South Australian gulf waters: an investigation of diet as a contributing factor. Honours thesis – Adelaide University. 66pp.

McGlennon, D., Kinloch, M.A. (1997). Resource allocation in the South Australian Marine Scalefish Fishery. FRDC Project 93/249, Final Report.

McIntosh, S. (1915). Fisheries Report of Chief Inspector for 1913-14. Adelaide, Australia: House of Assembly.

Myers, R.A., Worm, B. (2005). Extinction, survival or recovery of large predatory fishes. Philosophical Transactions of the Royal Society 1453: 13-20.

Parsons, D.M., Morrison, M.A., MacDiarmid, A.B., Stirling, B., Cleaver, P., Smith, I.W.G., Butcher, M. (2009). Risks of shifting baselines highlighted by anecdotal accounts of New Zealand's Snapper (*Pagrus auratus*) fishery. New Zealand Journal of Marine and Freshwater Research. 43: 965-83.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10: 430.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.J. Jr. (1998). Fishing down marine food webs. Science 279: 860-863.

Pepperell, J. (2018). Fishing for the past. Casting nets and lines into Australia's early colonial history. Rosenberg Publishing, Pty. Ltd. Australia.

PIRSA (2013). Management Plan for the South Australian Commercial Marine Scalefish Fishery. PIRSA Fisheries and Aquaculture, Adelaide, 143pp. The South Australian Fishery Management Series, Paper No. 59.

Sáenz-Arroyo, A., Roberts, C.M., Torre, J., Cariňo-Olvera, M., Hawkins, J.P. (2006). The value of evidence about past abundance: Marine fauna of the Gulf of California through eyes of 16th to 19th Century travellers. Fish and Fisheries 7: 128-146.

Santich, B. (1998). McLaren Vale. Sea and Vines. Wakefield Press, South Australia.

Simms, B. (1988). The end of a gulf fishery. The Ben Simms story. Mushroom Graphics, Moonta, South Australia. 22 pp.

Steer, M., Besley, M. (2016). The licence amalgamation scheme: Taming South Australia's complex, multi-species, multi-gear marine scalefish fishery. Fisheries Research 183: 625-633.

Steer, M.A., Fowler, A.J., Ward, T.M., Jones, G.K., Mayfield, S. (2014). The history of commercial fisheries of Spencer Gulf. In: Shepherd, S.A., Madigan, S.M., Gillanders, B.M., Murray-Jones, S., Wiltshire, D.J. (eds). In: Natural history of Spencer Gulf. pp 318-328.

Thomas, S. (2002). The Encounter, 1802. Art of the Flinders and Baudin Voyages. Art Gallery of South Australia, Adelaide.

Thurstan, R.H., Campbell, A.B., Pandolphi, J.M. (2016). Nineteenth century narratives reveal historic catch rates for Australian Snapper (*Pagrus auratus*). Fish and Fisheries 17: 210-225.

Wallace-Carter, E. (1987). For they were fishers. Amphitrite Publishing House, Australia. 408 pp.

1.6 Appendices

1.6.1 Commercial fishery statistics for regional populations

The following series of figures summarise the commercial fishery statistics that relate to South Australia's Snapper fishery. They are based on the information provided in the monthly catch returns of the commercial fishers that relate information about their fishing catches as well as the spatial and temporal aspects of their fishing operations. The data were provided for the 36-year period from 1984 to 2019 at the spatial scale of the regional population that comprise the stocks in the South Australia fishery. These were: for NSG, SSG and the WC for the Spencer Gulf/West Coast Stock; NGSV and SGSV for the Gulf St. Vincent Stock; and for the population of the SE Region that is the western-most population of the cross-jurisdictional WVS. Estimates of catch and effort were used to estimate catch per unit effort (CPUE), as an indicator of fishable biomass. As this species is captured when purposely targeted and as bycatch when other demersal fish species are targeted, its catches involve both targeted and non-targeted components. As it is difficult to ascribe levels of fishing effort to the non-targeted components of total catches, and because the targeted fishing statistics are likely to provide the best indicators of fish abundance, apart from total catch only the targeted fishing statistics are provided here. The catch and effort data provided by individual fishers were accumulated to calculate annual, regional totals for each year from 1984 to 2019 for both the handline and longline sectors. The gear-specific estimates of targeted catch were divided by the targeted effort to calculate annual estimates of CPUE. Furthermore, the numbers of commercial fishers who targeted Snapper with each gear type in each year were also provided.

Northern Spencer Gulf

Total catch from NSG has varied cyclically with peaks in 1990, 1999 and 2010, and low catches recorded in 1987, 1994 and 2005 (Fig. A1.1a). The highest catch of 360 t was recorded in 1999, after which there has been a general decline, particularly in 2012. Low catches persisted until 2019 when it was 31 t. Targeted handline catch was highest between 1998 and 2002 with the highest of 319 t taken in 1999, which fell to only 21 t in 2019 (Fig. A1.1b). Targeted handline fishing effort has also decreased since 2002, with particular drops in 2005 and 2012 (Fig. A1.1c). Between 2002 and 2019, it fell from 3,405 to 297 fisherdays, a decline of 91.3%. From 1984 to 2011, targeted CPUE showed a long-term increasing trend, although varying cyclically in association with targeted catch (Fig. A1.1d). Then in 2012, it declined by 50.9% from 139 to 68.2 kg.fisherday^{-1}. Since then, it has varied around a moderate level. The number of licence holders who targeted snapper has shown a long-term decline from the highest number of 88 in 1992 to 28 in 2015 to only 18 in 2019.

Targeted longline catch peaked at 84 t in 1997 (Fig. A1.1g). It decreased regularly after that and in 2019 was at only 1.8 t, the lowest yet recorded. Longline fishing effort declined from 2,347 fisherdays in 1997 to only 33 fisherdays in 2019, i.e., a reduction of 98.6% (Fig. A1.1h). Targeted longline CPUE was relatively consistent until 2002 (Fig. A1.1i). Subsequently, it was highly variable, varying between 87.3 kg.fisherday^{-1} in 2007 and 24.3 kg.fisherday^{-1} in 2013. It increased to 55.1 kg.fisherday^{-1} in 2019, although the catch and effort levels from which the values were calculated in 2012 to 2019 were very low. The number of longline fishers who targeted snapper declined consistently from 53 in 1988 to only four in 2019 (Fig. A1.1j).

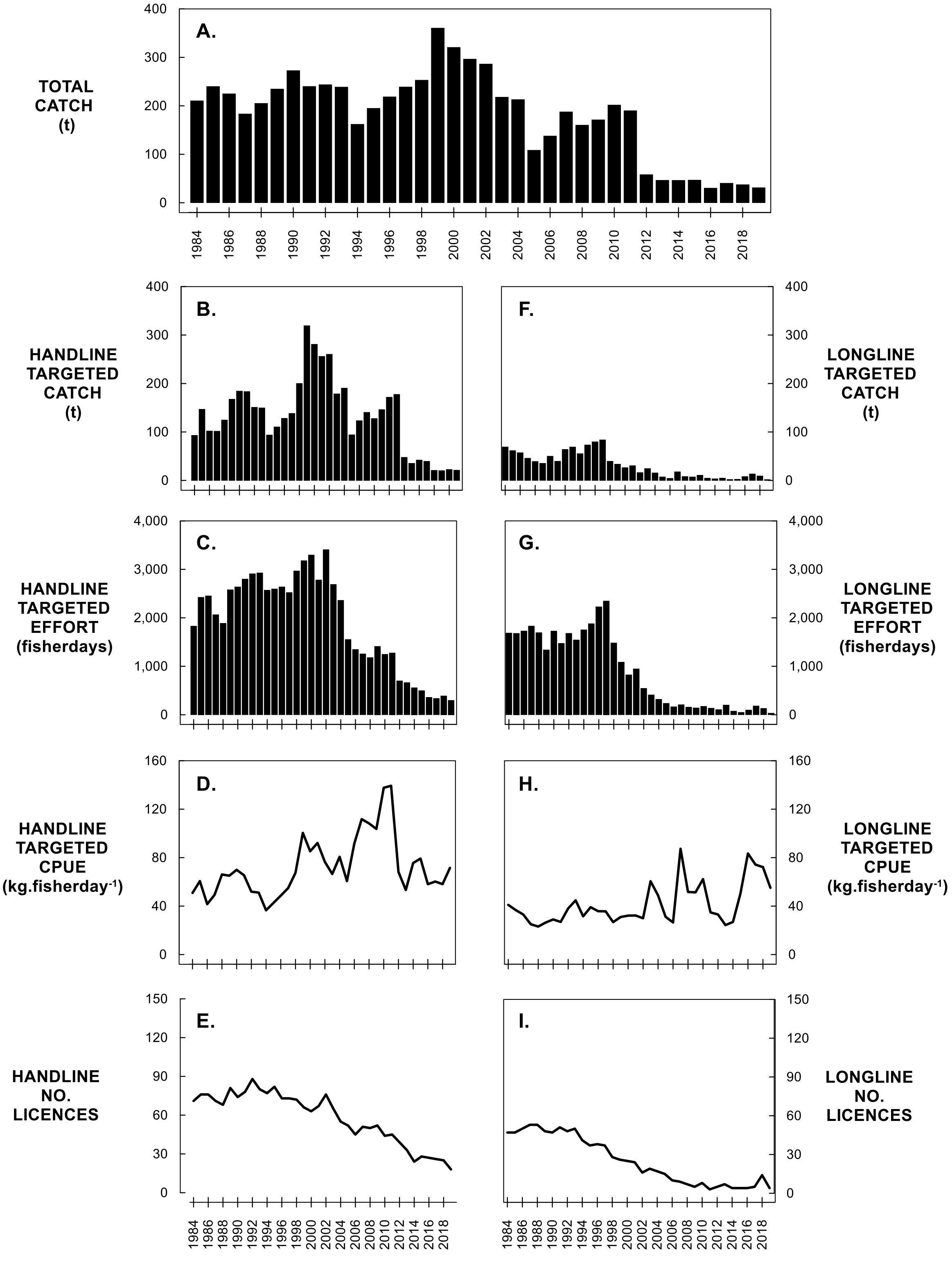


Fig. A1.1. Northern Spencer Gulf. a. Time series of total catch. Left hand graphs – time series for targeted handline sector. b. catch. c. effort. d. CPUE. e. number of licence holders who targeted Snapper. Right hand graphs – time series for targeted longline sector. f. catch. g. effort. h. CPUE. i. number of licence holders who targeted Snapper.

Southern Spencer Gulf

After low catches taken in SSG during the mid-1990s, total catch demonstrated two modes during the 2000s, the first peaked in 2001 at 294 t, whilst the second had a maximum of 402 t in 2007 (Fig. A1.2a). Total catch has subsequently declined regularly, falling to the lowest ever reported levels in 2018 and 2019. Targeted handline catch has been highly variable since the low catch of 1994 (Fig. A1.2b). It peaked at 251 t in 2001 and again at 237 t in 2007. Since then, it fell to 14 t in 2012, and further to only 2.3 t in 2019, the lowest recorded level. Targeted handline fishing effort has also varied cyclically, increasing from 559 fisherdays in 1994 to a peak of 1,637 fisherdays in 2001 (Fig. A1.2c). It has subsequently declined to the lowest level of only 65 fisherdays in 2019. Targeted CPUE peaked at 153 kg.fisherday^{-1} in 2001, and then at the record level of 180 kg.fisherday^{-1} in 2007 (Fig. A1.2d). However, from then until 2019, it declined by 80.4% to 35.3 kg.fisherday^{-1}. The numbers of fishers who targeted Snapper have been highly variable (Fig. A1.2e). They were particularly low through the mid-1990s, increased to their highest number of 87 in 2002, but then decreased consistently to the lowest number of 18 in 2019.

Targeted longline catch in SSG was very low until 2004, then increased rapidly in 2005 and peaked at 127.0 t in 2006 (Fig. A1.2g). It then declined substantially to only 6.5 t in 2019. The increase in catch between 2005 and 2009 was associated with a substantial increase in targeted fishing effort from 274 fisherdays in 2004 to 985 fisherdays in 2007, i.e., an increase of 259.5% (Fig. A1.2h). Nevertheless, since then, targeted effort has declined and in 2018 and 2019 was near the lowest level since the late 1990s. Targeted CPUE increased gradually through the late 1990s and early 2000s to around 70 kg.fisherday^{-1} (Fig. A1.2i). In 2005, it increased sharply to >120 kg.fisherday^{-1}, and remained at this high level until 2008. It has subsequently fallen considerably to the low value of 43.6 kg.fisherday^{-1} in 2019. The number of longline fishers that targeted Snapper in SSG was highest at 30 in 2007, when record catches and catch rates were taken and effort levels were highest (Fig. A1.2j). They have since decreased consistently to 14 fishers in 2019.

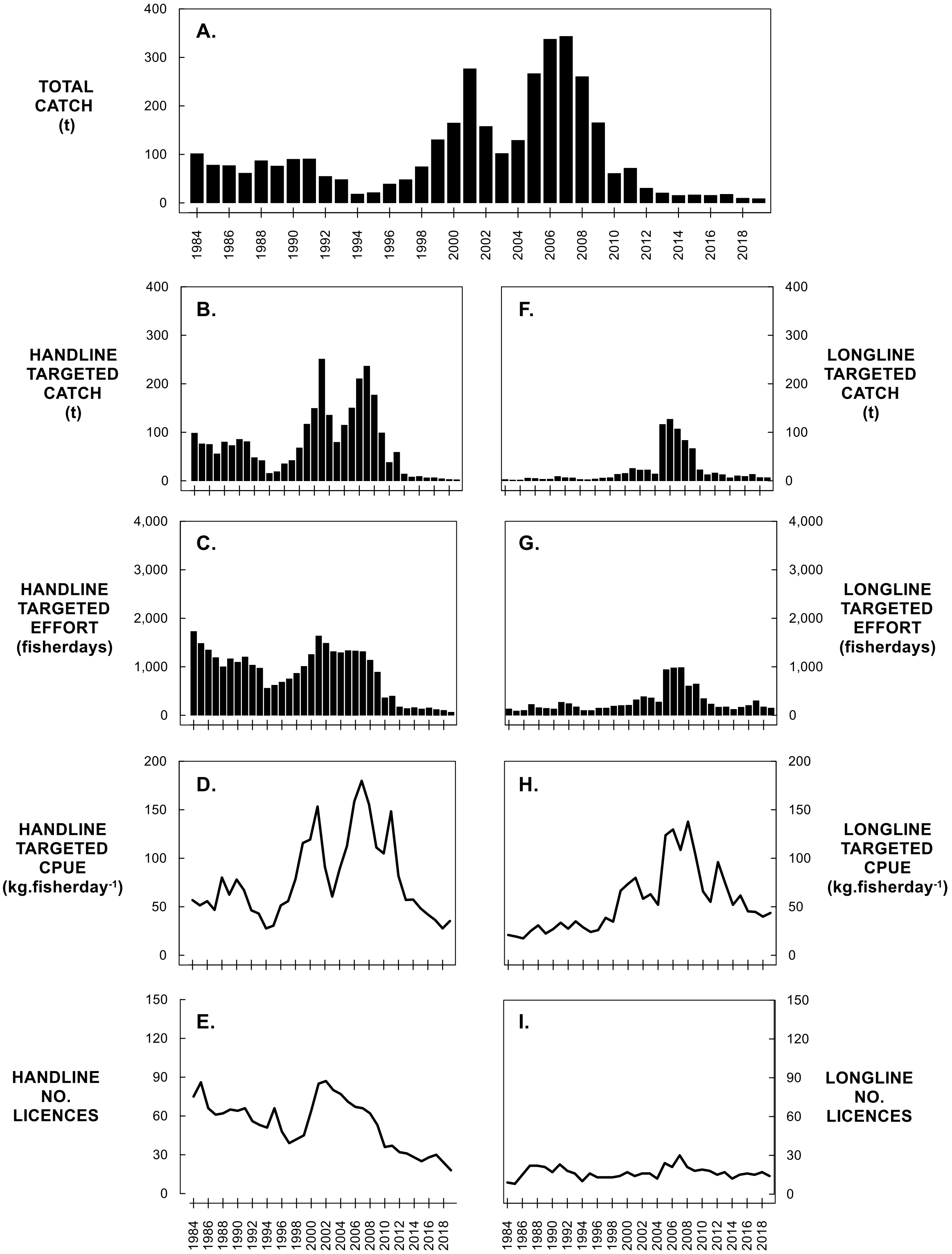


Fig. A1.2. Southern Spencer Gulf. a. Time series of total catch. Left hand graphs – time series for targeted handline sector. b. catch. c. effort. d. CPUE. e. number of licence holders who targeted Snapper. Right hand graphs – time series for targeted longline sector. f. catch. g. effort. h. CPUE. i. number of licence holders who targeted Snapper.

West Coast

The WC region has historically produced relatively low catches of snapper, nevertheless with some modes in production (Fig. A1.3a). The first peaked in the 1980s and then declined to low levels in the mid-1990s. The latter peaked in 2008 at 50.6 t. Since then, total catch has declined to 19.6 t in 2019. Targeted handline catch from the WC has generally been <12 t.yr^{-1} (Fig. A1.3b). It peaked in 2008 at 18.6 t.yr^{-1} and has subsequently fallen to only 2.6 t.yr^{-1} in 2019. Targeted handline effort has also been quite variable, but since 2005 has declined from 387 to 97 fisherdays (Fig. A1.3c). Targeted CPUE increased from 1995, peaking in 2008 and 2009 (Fig. 1.3d). It has subsequently fallen to 26.3 kg.fisherday^{-1} in 2019. The number of fishers who targeted snapper with handlines has shown two longterm cycles (Fig. A1.3e). There was a high period during the 1980s, when the number reached 36, which declined back to below 17 during the 1990s. They increased again in the late 1990s and early 2000s, peaking at 37 in 2001. Since then, there has been a gradual long-term decline back to 18 fishers in 2019.

Targeted longline catch was relatively low until the early 2000s when it increased to peak at 25.7 t.yr^{-1} in 2005 (Fig. A1.3g). Targeted effort displayed similar variation, increasing to a maximum of 605 fisherdays in 2009, before declining to 340 fisherdays in 2019 (Fig. A1.3h). Targeted CPUE increased after 1998 reaching a maximum of 93.4 kg.fisherday^{-1} in 2003 (Fig. A1.3i). It has then decreased to the minimum of 25.8 kg.fisherday^{-1} in 2013, apart from the spike in 2011. From 2013, LL CPUE had gradually increased to 52.0 kg.fisherday^{-1} in 2018. The number of longline fishers who targeted Snapper varied considerably between 1984 and 2019 (Fig. A1.3j). However, the number was highest between 2006 and 2017, peaking in 2008 at 31 fishers, and has subsequently declined to 17 fishers in 2019.

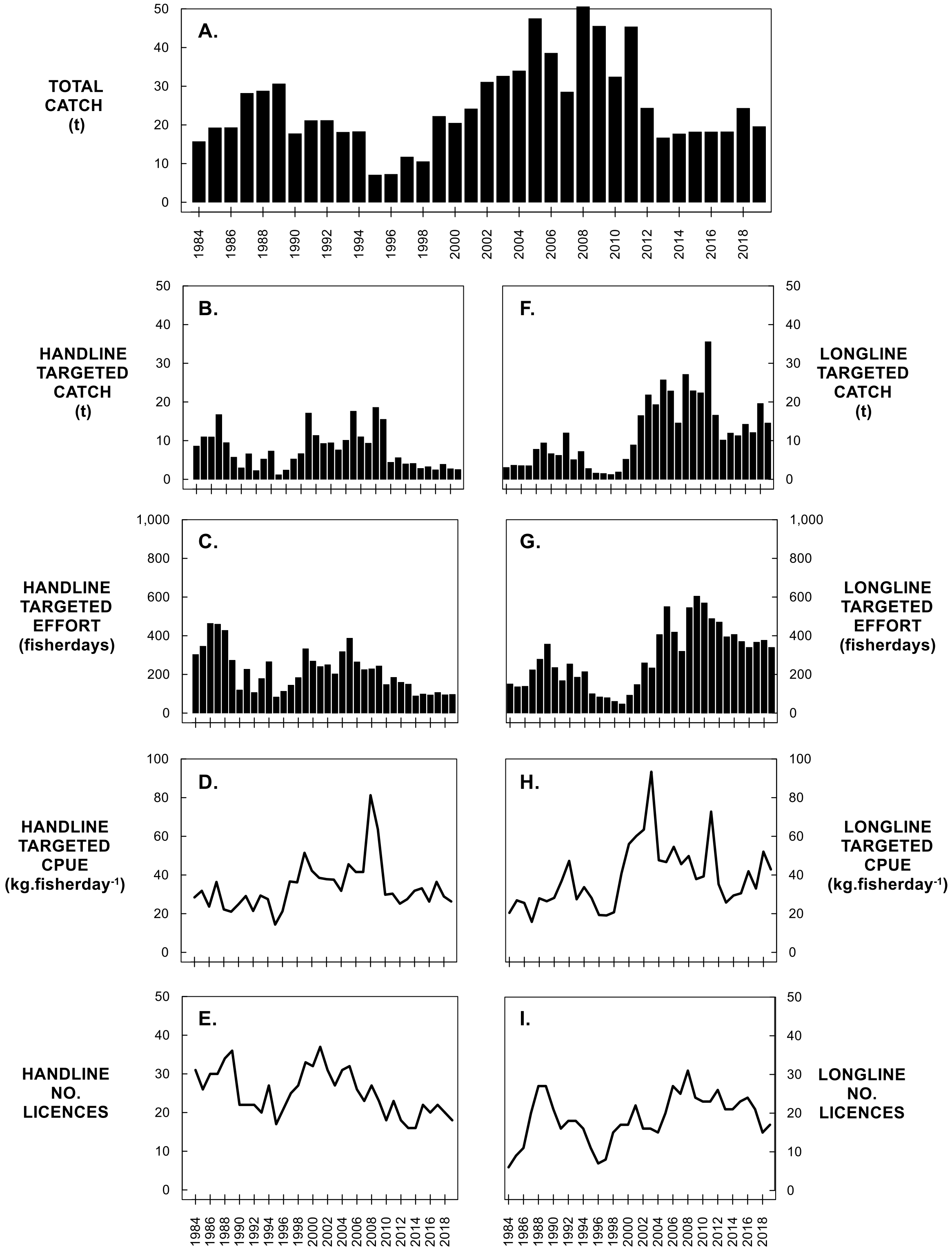


Fig. A1.3. West Coast of Eyre Peninsula. a. Time series of total catch. Left hand graphs – time series for targeted handline sector. b. catch. c. effort. d. CPUE. e. number of licence holders who targeted Snapper. Right hand graphs – time series for targeted longline sector. f. catch. g. effort. h. CPUE. i. number of licence holders who targeted Snapper.

Northern Gulf St. Vincent

Historically, NGSV produced only very low catches from the 1980s to early 2000s (Fig. A1.4a). However, from 2007 to 2010, total catch increased exponentially, culminating in the record catch of 417 t in 2010. Since 2015, total catch has declined considerably, dropping to 54.2 t.yr^{-1} in 2019. This has subsequently declined marginally to 380 t in 2015. Targeted handline catch in this region was generally low at <15 t.yr^{-1} up to 2006 and peaked at 52.7 t.yr^{-1} in 2010 (Fig. A1.4b). It has subsequently declined considerably to 3.1 t.yr^{-1} in 2019. The higher catches to 2010 were associated with an increase in targeted handline effort from 2004 to the maximum of 683 fisherdays in 2010 (Fig. A1.4c). This has subsequently declined to only 52 fisherdays in 2019. Targeted handline CPUE was relatively stable until 1996, after which it was variable, but nevertheless showed a long-term increase to a maximum of 99.0 kg.fisherday^{-1} in 2012 (Fig. A1.4d). Since then it has declined by 40.5% to 58.9 kg.fisherday^{-1} in 2019. The number of handline fishers that targeted Snapper in NGSV increased from 12 in 2003 to 28 in 2009, but has subsequently declined to 11 in 2019.

The longline fishery in NGSV has largely accounted for the recent rapid increase in total catch. Between 2008 and 2012, targeted longline catch increased by 873.5% from 37.0 to 360.6 t, and continued to increase to 370.7 t in 2015 (Fig. A1.4g). This increase was associated with a 543.1% increase in longline fishing effort from 390 to 2,508 fisherdays.yr^{-1} in 2015 (Fig. A1.4h). Longline CPUE demonstrated a long-term increase primarily between 2000 and 2010, when it peaked at 160.5 kg.fisherday^{-1} (Fig. A1.4). It has gradually declined to 135.2 kg.fisherday^{-1} in 2019. The number of fishers who used longlines to target snapper in NGSV increased from 11 in 2007 to 50 in 2011 and 2012 but has declined to 15 in 2019 (Fig. A1.4j).

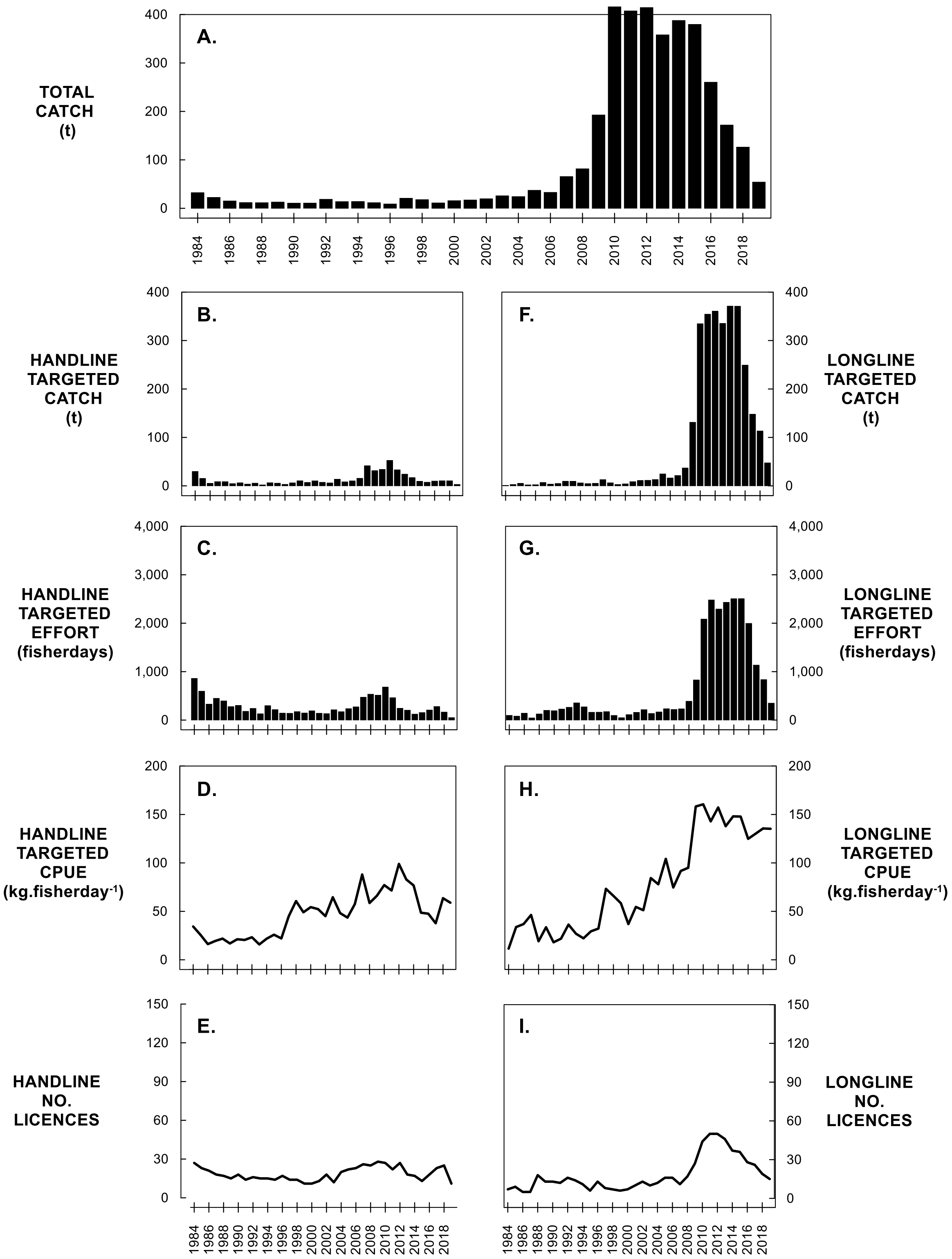


Fig. A1.4. Northern Gulf St. Vincent. a. Time series of total catch. Left hand graphs – time series for targeted handline sector. b. catch. c. effort. d. CPUE. e. number of licence holders who targeted Snapper. Right hand graphs – time series for targeted longline sector. f. catch. g. effort. h. CPUE. i. number of licence holders who targeted Snapper.

Southern Gulf St. Vincent

The regional fishery in SGSV is characterised by relatively low catches (Figs. A1.5a). Annual catches of around 80 t.yr^{-1} were taken through the 1980s, but subsequently ranged from 20 – 40 t.yr^{-1}. In the period of 2009 to 2011, relatively high annual catches of around 38 t were taken, but they subsequently declined to 27 t in 2015. Then from 2016, they gradually increased to the record catch of 117 t in 2019. The targeted handline fishery in SGSV produced its highest catches in the 1980s and early 1990s, before dropping to a low of only 4.7 t in 1995 (Fig. A1.5b). Since then there has been some cyclical variation but nevertheless has remained low at <20 t.yr^{-1}, particularly between 2008 and 2015. Targeted handline effort also declined between 1984 and 1995, and has remained low, particularly between 2008 and 2015 (Fig. A1.5c). Targeted CPUE was variable but increased consistently between 1995 and 2007, reaching a peak of 46.5 kg.fisherday^{-1} (Fig. A1.5d). It declined significantly to 20.8 kg.fisherday^{-1} in 2012 before increasing again to 29.9 kg.fisherday^{-1} in 2019. The number of handline fishers who targeted Snapper declined from 70 in 1985 to 17 in 2000 and has remained low until 2019 (Fig. A1.5e).

Targeted longline catch remained at <12 t.yr^{-1} until 2009 when it increased to 18.4 t (Fig. A1.5g). From 2016 to 2019, it increased from 44.4 to the record level of 102 t.yr^{-1}. Effort was relatively stable at <250 fisherdays.yr^{-1} between 1997 and 2004, but increased to 549 fisherdays in 2011 (Fig. A1.5h), corresponding to the period of expansion of longline fishing in NGSV. After decreasing for a couple of years, between 2014 and 2019, targeted effort increased considerably to the record level of 1,137 fisherdays. Targeted longline CPUE demonstrated a general increasing trend between 1996 and 2010 from 15.2 kg.fisherday^{-1} to a record level of 68.5 kg.fisherday^{-1} (Fig. A1.5i). In 2012, it declined to 31.5 kg.fisherday^{-1} before increasing considerably over several years to 89.7 kg.fisherday^{-1} in 2019. The number of longline fishers who targeted Snapper was as high as 25 between 2010 and 2012 but has subsequently declined to 19 in 2019 (Fig. A1.5j).

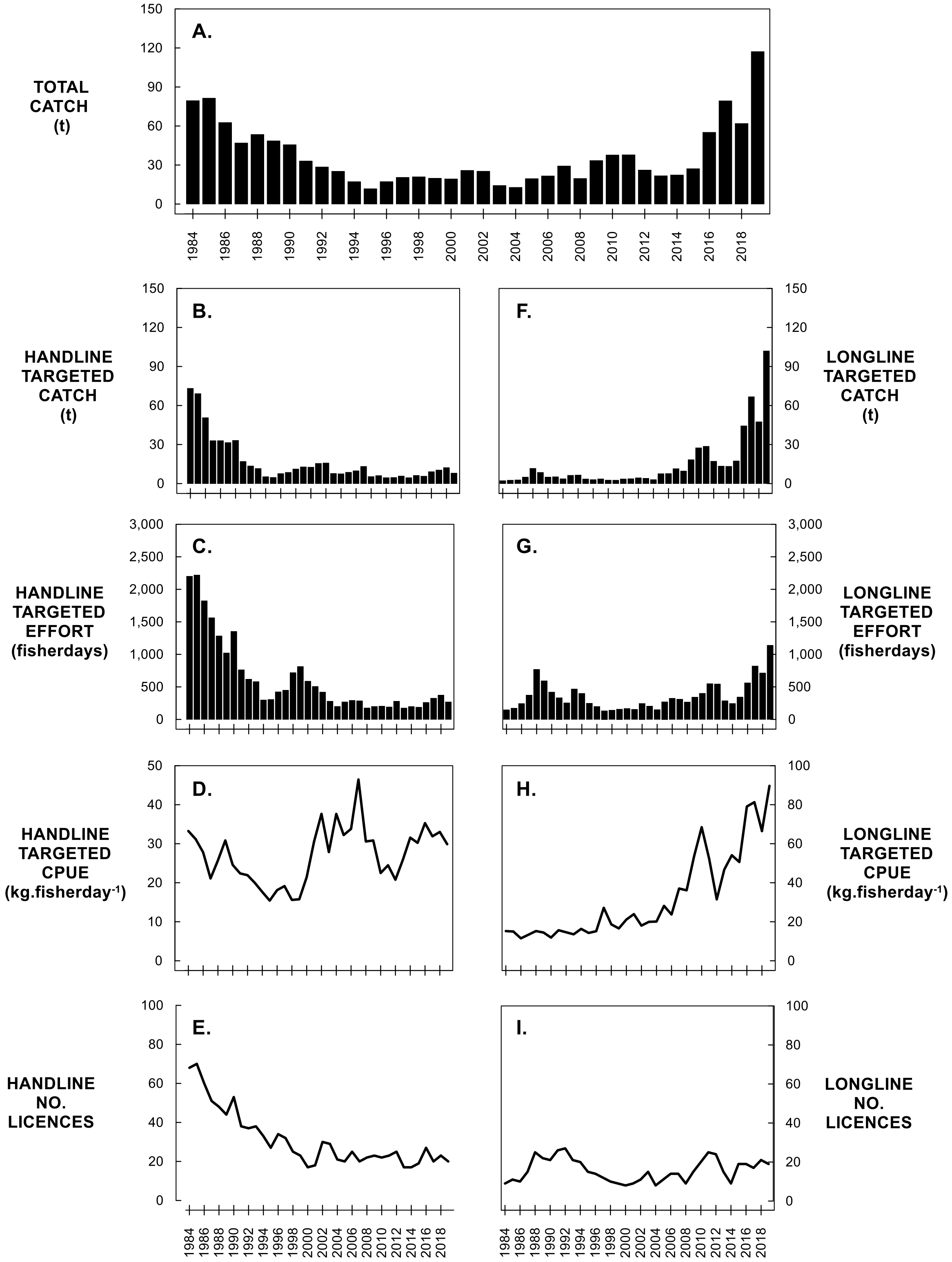


Fig. A1.5. Southern Gulf St. Vincent. a. Time series of total catch. Left hand graphs – time series for targeted handline sector. b. catch. c. effort. d. CPUE. e. number of licence holders who targeted Snapper. Right hand graphs – time series for targeted longline sector. f. catch. g. effort. h. CPUE. i. number of licence holders who targeted Snapper.

South East Region

Historically, the SE region produced only marginal catches of Snapper (Fig. A1.6a). However, from 2006 to 2010 there was an exponential increase that culminated in the record catch of 261 t in 2010. Since then, it declined regularly back to 9.4 t in 2017 before increasing marginally to 18.4 t in 2019. Targeted handline catch in the SE has always been low (Fig. A1.6b). There was a minor increase to >10 t.yr^{-1} between 2006 and 2009, which has subsequently declined to approximately 1 t.yr^{-1} between 2013 and 2019. Such catches reflect low but variable fishing effort, which declined from 300 fisherdays in 2007 to only 23 in 2019 (Fig. A1.6c). Between 1984 and 2002, CPUE was less than 20 kg.fisherday^{-1}. From 2003 it increased and was highest from 2006 to 2009, reaching a maximum of 54.0 kg.fisherday^{-1}. It declined to a minimum in 2017 before increasing quickly in 2019. The number of fishers who targeted Snapper was variable up to 2009, although generally <10 before declining to only three fishers in 2016 (Fig. A1.6e). In 2019, there were six handline fishers.

Targeted longline catches were always less than several tonnes.yr^{-1} up to 2007 (Fig. A1.6g). From then, there was a rapid increase to the maximum level of 239 t in 2010, which subsequently declined to 3 t in 2016 before increasing to 16 t in 2019. Over the same period there was a considerable increase in targeted longline effort, which peaked in 2010 at 2,608 fisherdays, but which has subsequently declined to 198 fisherdays in 2019 (Fig. A1.6h). Targeted CPUE also increased dramatically from 2007 to 2010, peaking at 91.6 kg.fisherday^{-1}. Subsequently, it has been quite high but nevertheless also quite variable. The number of longline fishers who targeted Snapper increased dramatically from 2005 peaking at 25 in 2010 before declining gradually to 9 fishers in 2019 (Fig. A1.6j).

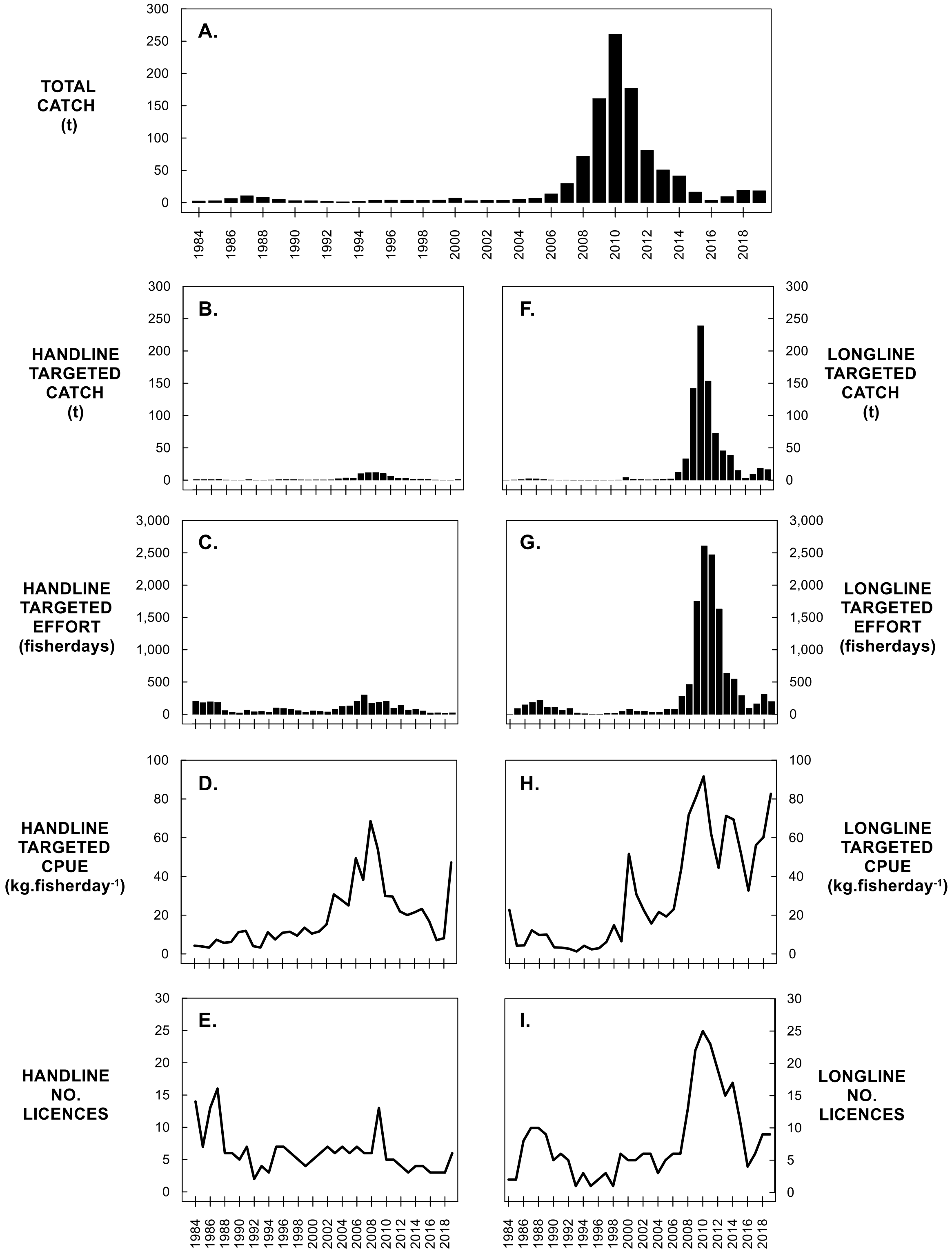


Fig. A1.6. South East Region. a. Time series of total catch. Left hand graphs – time series for targeted handline sector. b. catch. c. effort. d. CPUE. e. number of licence holders who targeted Snapper. Right hand graphs – time series for targeted longline sector. f. catch. g. effort. h. CPUE. i. number of licence holders who targeted Snapper.

2. REPRODUCTIVE BIOLOGY – SPAWNING FRACTIONS

2.1 Introduction

Different species of fish employ different strategies to maximise their reproductive success. The reproductive strategy of any fish species is an essential part of its life history strategy that contributes to its population replenishment processes and population dynamics. For exploited species, this also contributes to its fishery productivity. As such, for fishery scientists, understanding the reproductive biology of a species is fundamental to developing the appropriate fishery management strategy, to ensure the sustainability of its fishery. The different reproductive strategies are manifested in the processes of oogenesis, the behavioural aspects of spawning and the seasonality of reproduction. The diversity in the processes of oogenesis are manifested in the different cellular processes of oocyte growth and development, the sizes of the oocytes, their dynamic organisation within the ovarian matrix, and the process and rate of atresia of unspawned oocytes (Wallace and Selman 1987). Most species of fish demonstrate seasonality in their reproductive biology, i.e., an annual cycle during which reproductive activity is restricted to a consistent period of the year. This represents a highly evolved system that entails the entrainment of the physiology of the species to seasonal variation in environmental conditions. Such seasonality is thought to be a mechanism to ensure that the resulting larvae hatch into physical environmental conditions that optimise their chances of survival (Sheaves 2006). There is considerable evidence that the most significant environmental stimuli to which fish physiology is entrained are photoperiod and water temperature (Pankhurst and Port 2003, Pankhurst and Munday 2011).

Snapper (*Chrysophrys auratus*) are distributed broadly throughout the nearshore coastal waters of Australia and New Zealand, occupying a diversity of marine habitats (Kailola et al. 1993). The reproductive biology of Snapper has been considered at several places that demonstrate different environmental conditions, such as New Zealand, Western Australia and Spencer Gulf, South Australia (Scott and Pankhurst 1992, Scott et al. 1993, McGlennon 2003, Wakefield et al. 2010, Saunders et al. 2012). These studies have identified several consistencies in the reproductive strategy. Snapper demonstrate asynchronous oocyte development, have indeterminate fecundity and are iteroparous, with individuals participating in multiple batch spawning events throughout potentially numerous spawning seasons (Saunders et al. 2012). Nevertheless, across the broad range of Snapper, several regional differences in the reproductive biology have been identified which imply differences in the physiological/environmental interactions. These include the seasonality of spawning and the duration of the spawning seasons. For understanding population dynamics and developing appropriate fishery management strategies, they indicate the need to consider the reproductive biology of Snapper at a regional scale.

In South Australia, Snapper is an important fishery species that is managed as part of the Marine Scalefish Fishery. Throughout the mid-2000s, it was the dominant State-based contributor to the national total catches of Snapper combined across the commercial and recreational sectors (Fowler et al. 2016). Nevertheless, from 2011 onwards, changes in the statuses and the spatial structure of the State's regional fisheries led to the need to consider the management strategy (Fowler et al. 2016; Fowler et al. 2019; Fowler et al. 2020, Drew et al. 2022). From 2012 onwards, an escalating series of management changes was implemented to address the concerns. These changes were designed to limit commercial catches and to maximise opportunities for spawning and recruitment success. The changes to the management practises implemented throughout the 2000s, forced the need to consider fishery status indicators that were independent of the fishery-related data (Fowler et al. 2020). The daily egg production method (DEPM) for estimating spawning biomass had previously been successfully applied for Snapper populations in New Zealand (Zeldis 1993, Zeldis and Francis 1998) and Western Australia (Jackson and Cheng 2001). It had previously also been applied in South Australia in the 1990s (McGlennon 2003), but then unsuccessfully in the early 2000s (Fowler unpublished data). Through the latter 2000s, an FRDC-funded project investigated modern methods for applying the DEPM for Snapper in South Australia (Steer et al. 2017), which has allowed the DEPM to become part of the stock assessment process (Fowler et al. 2019, Fowler et al. 2020, Drew et al. 2022).

The DEPM is used to estimate the biomass of the spawning component of a fish population by empirically combining the estimates of the density of pelagic eggs and the estimates of a range of adult parameters that relate to the reproductive biology of the target species, which include the sex ratio, spawning fraction and the batch fecundity (Lasker 1985). The empirical approach required to attain estimates of these various parameters depends on intensive sampling of the adult fish (Steer et al. 2017). Whilst for Snapper, attaining estimates of sex ratio and batch fecundity have been relatively straight-forward, it has been more problematic to provide estimates of spawning fraction. This requires differentiating between 'immature' and 'mature' fish; and for dividing the latter category into the 'spawning' and 'non-spawning' components. The terms 'maturity' and 'spawning' have different temporal connotations. Those relating to 'maturity' refer to whether a female has or will spawn during the current reproductive season, and so relate to the time scale of numerous weeks to months. Alternatively, whether a fish is 'spawning' relates to the current 24-hour period, with respect to whether spawning has occurred in recent hours or will likely occur in the next few hours. Identifying 'spawning' fish can be quite technically challenging as it requires understanding: the microscopic changes that occur in ovaries on a diurnal basis associated with oocyte maturation and spawning; as well as the relationship between such changes at the microscopic scale in the ovary and the external macroscopic appearance of the ovaries.

The spawning fraction of a sample of fish reflects the proportion of mature females that have or will spawn in the current 24-hour period. Having such information is important in the application of the DEPM for estimating spawning biomass as it provides an estimate of the proportion of the mature females that contributed to the current egg density that was measured during the plankton sampling regime. For Snapper in South Australia, there is considerable variation in the estimates of spawning fraction within and between seasons, based on studies to date (McGlennon 2003, Saunders et al. 2012). Determining the spawning fraction for a sample of fish depends on macroscopic analysis of all ovaries followed by microscopic analysis for selected ones for which there is some ambiguity about their spawning status.

Throughout the 1990s and 2000s, several studies were undertaken in South Australia during which adult sampling of Snapper provided estimates of spawning fraction for one or several regions (McGlennon 2003, Saunders et al. 2012, Fowler unpublished data). On several occasions, these studies contributed to attempts to apply the DEPM to estimate spawning biomass. Here, the data from these various studies, based on samples of adult Snapper that were captured from different places and times, have been brought together. The purpose is to consider estimates of spawning fraction at the spatial scales considered in the different studies to determine whether there are any consistent spatial or temporal patterns that would provide useful contextual information for future applications of the DEPM methodology. The broadest spatial sampling of adult Snapper that provided estimates of spawning fraction was undertaken during the 2019/20 and 2021/22 reproductive seasons, when several gulf-based regions were considered. Here, the estimates of reproductive parameters for these regions are considered in detail. Also presented are the historical estimates of spawning fraction from the earlier studies.

2.2 Materials and methods

2.2.1 History of studies on reproductive biology

Throughout the history of research on the Snapper fishery in South Australia, there have been several periods during which the reproductive biology was comprehensively analysed (Table 2.1). These studies have involved not only the macroscopic analysis of the gonads but also for some ovaries consideration of the microscopic characteristics based on histological analysis. The regions considered were Northern Spencer Gulf (NSG) and Southern Spencer Gulf (SSG) that were divided at the 34°S latitude and Northern Gulf St. Vincent (NGSV) and Southern Gulf St. Vincent (SGSV), as divided at the 35°S latitude (Fig. 2.1). Prior to 2019/20, all such sampling had been concentrated in Spencer Gulf, particularly NSG. In the summers of 2019/20 and 2021/22, the regions of NGSV and SGSV were also considered.

Table 2.1. Summary of studies undertaken on the reproductive biology of Snapper in South Australia that have considered both the macroscopic and microscopic characteristics of the ovaries. NSG – Northern Spencer Gulf; SSG – Southern Spencer Gulf; NGSV – Northern Gulf St. Vincent; SGSV – Southern Gulf St. Vincent; Comm – commercial; Rec – recreational.

Region	Date	Number of females	Sample types	Reference
NSG	Nov 1994	64	Comm, Rec	McGlennon 1994
NSG	Dec 1994	109	Comm, Rec	McGlennon 1994
NSG	Dec 1995	149	Comm, Rec	McGlennon 1994
NSG	Jan 1996	363	Comm, Rec	McGlennon 1994
NSG	2000	1,076	Comm	Fowler (unpublished)
NSG	2001	596	Comm	Fowler (unpublished)
NSG	2002	190	Comm	Fowler (unpublished)
SSG	2000	400	Comm	Fowler (unpublished)
SSG	2001	273	Comm	Fowler (unpublished)
SSG	2002	88	Comm	Fowler (unpublished)
NSG	2005	506	Comm, Charter, Res	Saunders (2009), Saunders et al. (2012)
NSG	2006	540	Comm, Charter, Res	Saunders (2009), Saunders et al. (2012)
NSG	2007	454	Comm, Charter, Res	Saunders (2009), Saunders et al. (2012)
NSG	2008	56	Comm, Charter, Res	Saunders (2009), Saunders et al. (2012)
NSG	2019	366	Res	Fowler et al. (2020)
NGSV	2020	200	Comm	Fowler et al. (2020)
SGSV	2020	297	Comm	Fowler et al. (2020)
SSG	2020	274	Comm	Fowler et al. (2020)
NSG	2021	356	Comm	Drew et al. (2022)
SSG	2021	147	Comm	Drew et al. (2022)
NGSV	2022	264	Comm	Drew et al. (2022)
SGSV	2022	216	Comm	Drew et al. (2022)

2.2.2 Sample processing

The studies identified in Table 2.1 were done over nearly 30 years during which there was continuity amongst the personnel in the research teams, providing consistency in the methods of sample processing. Adult Snapper were accessed through the commercial, recreational and charter boat sectors, as well as by scientific teams during research field trips. Snapper were processed as soon as possible after capture, generally within 24 hours of their removal from the water. Where possible, each fish was measured for caudal fork length (CFL), weighed and the otoliths were removed to later determine fish age. The gonads were removed, sexed, and weighed for calculation of gonosomatic indices. The ovaries were then classified macroscopically to stage of development based on their size, colour, and visibility of oocytes (Table 2.2) (photographs of whole ovaries classified to Stages 3, 4 and 5 are presented in Appendix 2.6.1). Some ovaries were then selected for histological analysis. For these, a small segment was removed from the centre of one ovary, placed in a small histological capsule and then preserved in a fixative solution of formalin, acetic acid and calcium chloride (FAACC).

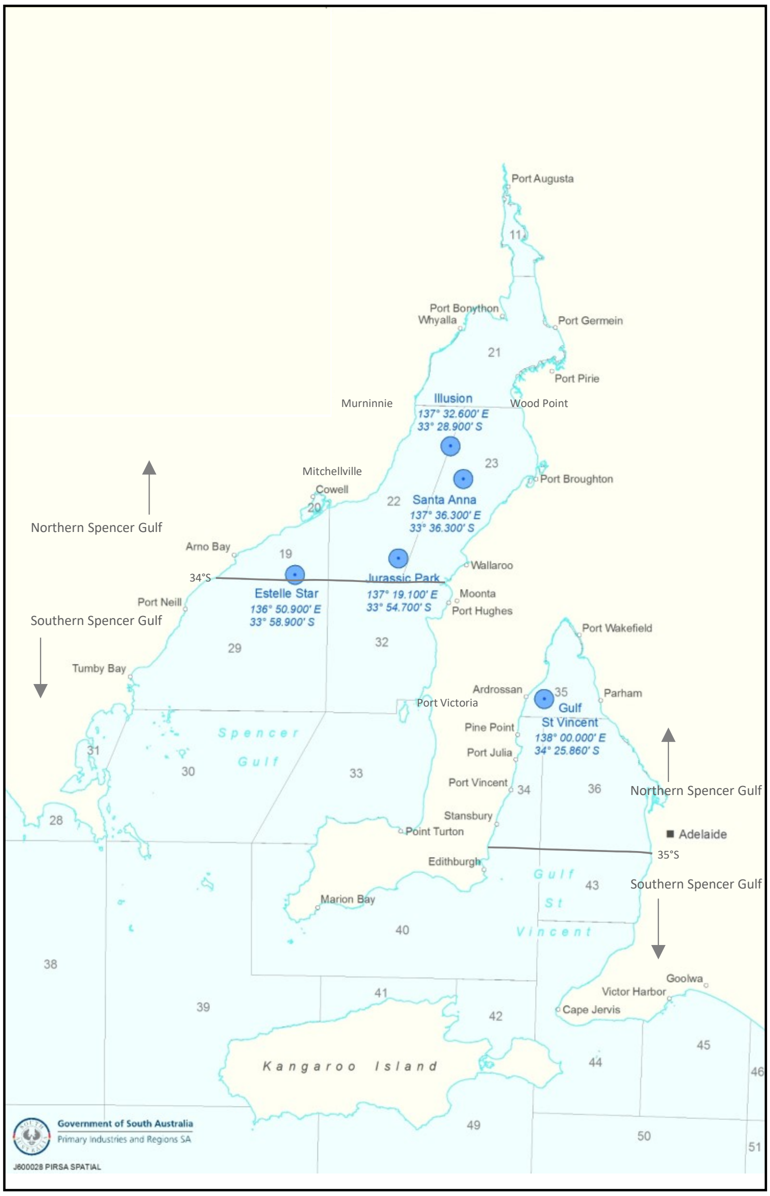


Fig. 2.1. Map of the gulf region of South Australia, showing a number of the fishing locations and ports-of-landing referred to in the text with respect to estimating spawning fractions.

Table 2.2. Criteria assessed to determine spawning fraction based on the macro-analysis of the ovaries of Snapper. Also shown are the microscopic characteristics of ovaries at each stage, based on the analysis of histological slides, considering the stages of oocyte development presented in Table 2.3.

Stage	Maturity?	Spawning?	Macroscopic appearance of ovary	Microscopic characteristics from histological preparations
1	No	No	Ovary small, undeveloped, clear.	Only unyolked and non-atretic oocytes.
2	Yes	No	Ovary small, opaque, light yellow in colour, individual oocytes not discernible.	Mainly unyolked and some partially yolked oocytes.
3	Yes	??	Ovaries relatively large, yellow to orange in colour, individual oocytes discernible.	Dominant oocyte stage is advanced yolked oocyte. Some oocytes may be atretic.
4	Yes	Yes	Ovaries large, yellow to orange. Clear, large translucent hydrated oocytes visible amongst smaller opaque ones. Oocytes may be ovulated, i.e. located in the oviduct.	Oocytes at all stages from unyolked to hydrated. Also, atretic advanced yolked oocytes and post ovulatory follicles may be present.
5	Yes	No	Ovary reduced in size, flaccid, yellow to pink to dark brown.	Atretic vitellogenic oocytes outnumber vitellogenic ones. Pre-vitellogenic oocytes also present.

Table 2.3. Descriptions of each stage of development of oocytes, α-atretic oocytes and post-ovulatory follicles (modified from Hunter and Macewicz 1985).

Stage	Microscopic characteristics from histological preparations
1 - Unyolked	Oogonia small, cytoplasm basophilic, nuclei large, centrally located, several nucleoli occur at the periphery of the nucleus.
2 – Partially yolked	Similar to Stage 1, but larger (mean = 211 µm, range 156-312 µm, n = 392, 10 ovaries). Clear lipid granules throughout cytoplasm. Follicular layer comprises two cell layers. Zona radiata present but thin.
3 – Advanced yolked	Oocytes large (mean = 351 µm, 204 - 555 µm, n = 756, 10 ovaries). Lipid granules and eosinophilic yolk protein granules throughout the cytoplasm. Nucleus still centrally located. Zona radiata thick and highly eosinophilic.
4 – Migratory nucleus	Similar to Stage 3 oocytes except nucleus is migrating or has migrated to the peripheral cytoplasm. This represents the initiation of the hydration process.
5 - Hydrated	Oocytes much larger (mean = 822 µm, 720 – 974 µm, n = 352, 10 ovaries) with uptake of fluid. Nucleus absent. Yolk plates occupy entire volume of cytoplasm, then fuse to form a homogeneous mass. Zona radiata and follicular layers become greatly stretched.
α-atretic oocyte	Zona radiata dissolves, oocyte shape loses integrity. Yolk globules begin to disintegrate and are less regular in shape.
Post-ovulatory follicle (new)	Remaining follicle soon after ovulation is large, highly convoluted with an obvious lumen, and may contain fine granular material. The layered nature of both cell types (thecal and granulosa) remains intact.
Post-ovulatory follicle (old)	Convoluted nature much less apparent, lumen much reduced, even closed, and the thecal and granulosa cells no longer retain their orderly arrangement.

2.2.3 Laboratory Analysis of Samples

Histological slides were prepared from the FAACC-preserved tissue. The tissue was sectioned at 6-7 µm and stained with haemotoxylin and eosin. The slides were examined at x100 magnification and examined for: the most advanced stage of oocyte development; the level of atresia; and the presence/absence of post-ovulatory follicles (Farley and Davis 1998, Fowler et al. 1999, Saunders et al. 2012). The most advanced oocytes were classified as unyolked, partially yolked, advanced yolked, migratory nucleus or hydrated according to the criteria in Table 2.3, as evident in Figs. 2.2 and 2.3. The ranges in oocyte sizes at the different stages were determined from histological slides based on the sizes of numerous oocytes from 10 different ovaries (Fowler unpublished data). The presence/absence of post-ovulatory follicles was noted along with a qualitative assessment of their age, based on the presence/absence of a lumen and the level of disruption to the arrangement of the thecal and granulose cells (Table 2.3). The abundance of α-atretic advanced yolked oocytes relative to their abundance was estimated as: no atresia, <10%, 10-50%, >50% and 100%.

2.2.4 Micro and macro characteristics of ovaries – estimating spawning fraction

The differentiation of female Snapper into 'mature' and 'immature' fish was based on the macroscopic stage (Table 2.2), i.e., Stages 2 to 5 are considered mature. Differentiating whether a 'mature' fish was 'spawning' or 'non-spawning' fish, was straight-forward for those fish classified to Stages 2, 4 and 5 (Table 2.2). Those at Stages 2 and 5 would not have spawned in the current 24-hour period, whereas those at Stage 4 would have spawned within the next few hours. Nevertheless, for those at Stage 3, there was uncertainty about spawning status. To resolve this, the microscopic characteristics of the ovaries were considered from the histological slides. Ovaries at macroscopic Stage 3 were considered to be 'spawning' if: (1) there were migratory nucleus oocytes present, which represents the start of the hydration process; or (2) if there were new post-ovulatory follicles present. These two features indicate that spawning would have occurred at some time during the current day or that spawning had occurred in the recent few hours, respectively (Matsuyama et al. 1988). Here, the combination of microscopic features was interpreted to determine whether a fish was 'spawning' or 'not spawning'. Appendix 2.6.2 presents a series of photographs and photomicrographs which demonstrate the relationships between macroscopic appearance and microscopic characteristics of the ovaries at different stages of development.

Over the summers of 2019/20 and 2021/22, numerous samples of adult Snapper were collected from NSG, SSG, NGSV and SGSV. Because the fisheries in these regions were closed in November 2019 (Fowler et al. 2020), these samples were primarily provided by commercial fishers who were contracted to do so by SARDI. A few samples from NSG were accessed during DEPM research cruises. As SARDI personnel were associated with the collection of these latter samples, the period of the day during which each fishing operation was undertaken was known, although the exact time-of-capture of individual fish was not recorded. For the sampling during 2019/20, there was only limited spatial information recorded for each fishing operation. This meant that, overall, there was limited information for when and where each sample of fish was collected. For sampling undertaken in 2021/22, the details regarding fishing locations and approximate times of fishing operations were recorded. For each sample of fish collected from a region, a raw estimate of spawning fraction was calculated as the proportion of ‘mature’ fish that were ‘spawning’. This was then used to calculate a weighted estimate of spawning fraction by multiplying by a weighting factor (W) calculated as: $W = (n*a/N)$, where n = number of mature fish in the sample, a = number of samples considered for the region, and N = total number of mature fish across all samples. To provide a regional estimate of spawning fraction, the average of the weighted estimates for the individual samples was calculated.

In this chapter, the estimates of spawning fraction from studies done before 2019/20 were also considered (Table 2.1). Such studies were only done for NSG as during the 1990s and early 2000s the fishery was concentrated in this region. The purpose here was to consider whether there were any spatial or temporal patterns that might inform future applications of the DEPM methodology.

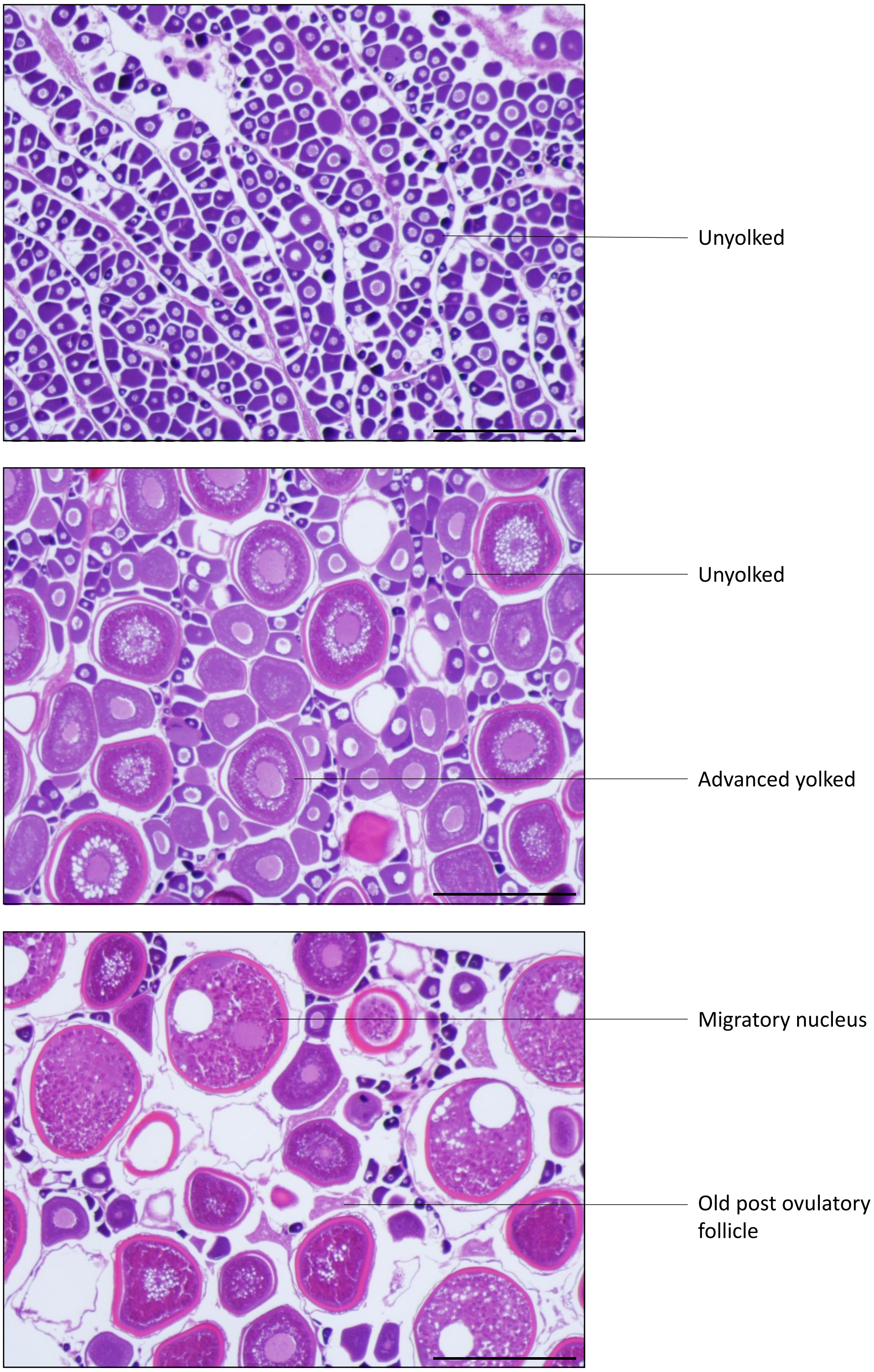


Fig. 2.2. Photomicrographs of histological slides prepared from Snapper ovaries collected from Spencer Gulf and Gulf St. Vincent in 2021 and 2022 demonstrating some of the microscopic features of the ovaries associated with maturation and spawning, i.e., the range of development stages of oocytes, stages of post-ovulatory follicles and atretic oocytes. Scale bar = 500 µm.

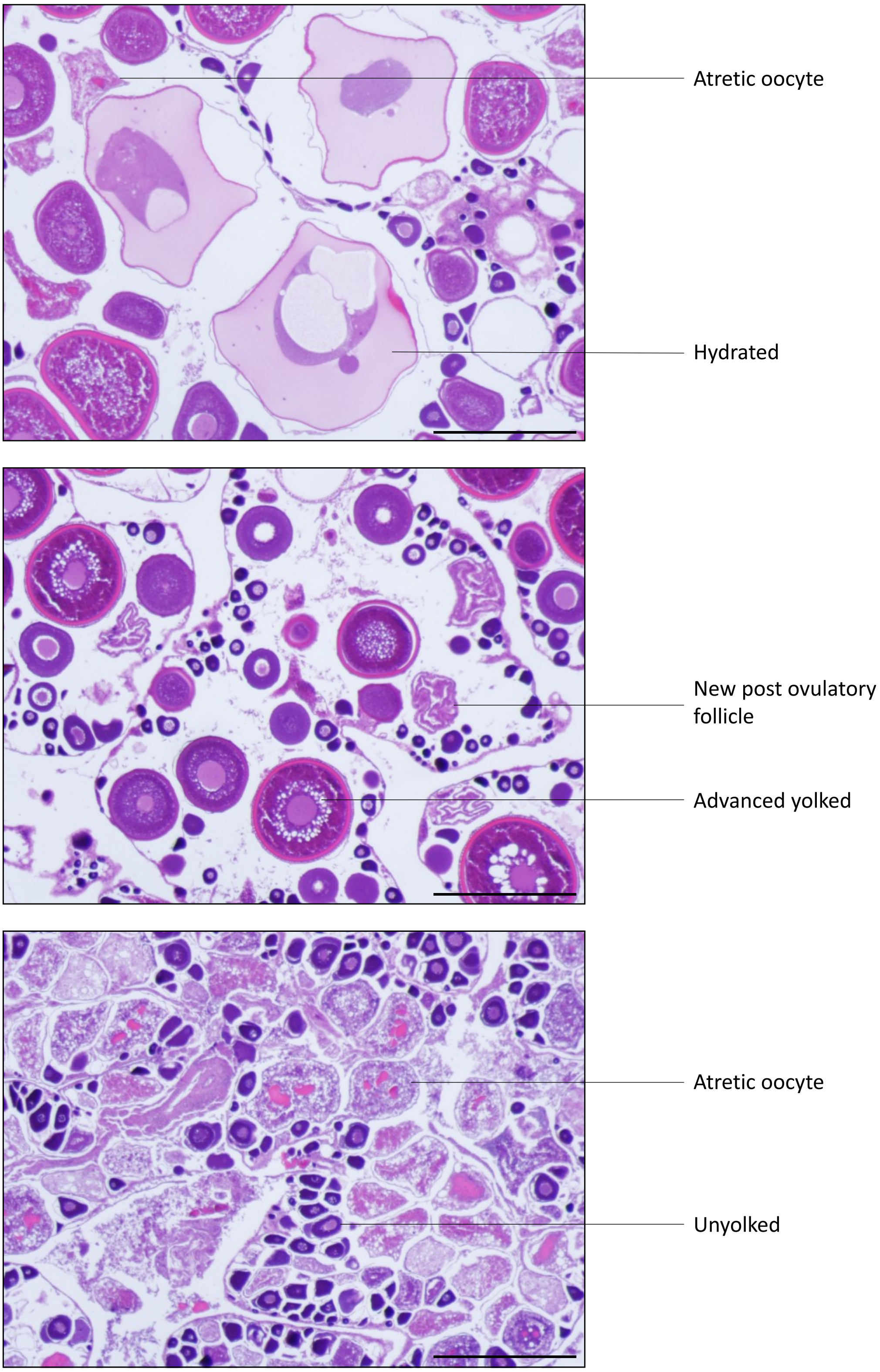


Fig. 2.2 cont'd. Photomicrographs of histological slides prepared from Snapper ovaries collected from Spencer Gulf and Gulf St. Vincent in 2021 and 2022 demonstrating some of the microscopic features of the ovaries associated with maturation and spawning, i.e. the range of development stages of oocytes, stages of post-ovulatory follicles and atretic oocytes. Scale bar = 500 µm.

2.3 Results

2.3.1 Estimates of reproductive parameters for 2019/20

Northern Spencer Gulf

Over approximately two weeks from the 5th to 18th December 2019, eight samples of adult Snapper were collected from several localities distributed throughout NSG (Table 2.4). The total number of fish sampled was 366, which included 186 females. Two samples were collected from the port-of-landing of Port Pirie (Fig. 2.1). These fish were associated with hard structure located in shallow water close to the eastern shoreline of the gulf, likely over sand flat or seagrass habitat. All females collected from these sites were classified macroscopically to Stages 1 and 2, i.e., for most fish maturation had commenced but none were spawning. Estimates of spawning fraction for both samples were zero.

The other localities from which samples of Snapper were collected from NSG between early and mid-December 2019 were from the vicinity of the wrecks of The Illusion, the Santa Anna, and the Estelle Star, as well as one sample from Port Broughton as the port-of-landing. These were all deep, offshore localities (Fig. 2.1). The 137 females were all classified to Stages 2, 3, and 4, i.e., all were mature, and some were spawning. However, histological analysis of the numerous ovaries that were classified to Stage 3 was not done, which compromised the capacity to accurately estimate the spawning fractions. Estimates of the maximum and minimum spawning fractions, were determined by considering only those classified to Stage 4 as spawning, were 0.8 and 0.14, respectively (Table 2.4).

Southern Spencer Gulf

The sampling of Snapper from SSG took place between 10th February and 11th March 2020, which involved seven fishing operations from Port Victoria (Table 2.4, Fig. 2.1). Whilst fishing took place in offshore waters that were up to several hours travel from port, apart from that this was done in MFAs 32 and 33 there is little detail about where fishing had occurred. A total of 274 adults were captured that included 136 females, all of which were classified to Stages 3, 4 or 5. The last sample collected on 11th March 2020 had the highest proportion of fish at Stage 5, suggesting that although some fish were still spawning at this late stage of the season, the reproductive season was coming to an end. Until the 29th February, a considerable proportion of females were reproductively active, with the estimates of spawning fraction ranging from 0.06 to 0.55 (Table 2.4). These were generally lower than the estimates obtained for other regions, reflecting the high number and proportion of fish classified to Stage 5 associated with the lateness in the season. The weighted estimates of spawning fraction were calculated, of which the regional average is 0.35.

Northern Gulf St. Vincent

From 17th January to 10th February 2020, there were six samples of adult Snapper collected from throughout NGSV, including the waters offshore from Stansbury and northwards to Black Point, Port Julia, as well as the wreck of the *Zanoni* (Table 2.4, Fig. 2.1). A total of 220 fish were sampled of which 126 were females. Most were mature, with only one fish classified to Stage 1. Those captured near Stansbury were taken from mid-January until early February and were classified to Stages 3, 4 and 5. The estimates of spawning fraction were 0.55, 0.79 and 0.39, for the three consecutive samples (Table 2.4). Each involved relatively high proportions of fish that were at Stage 5, particularly those taken on 4th February. The other three samples for this region were taken from localities on the north-western and north-eastern sides of the gulf. Those from the western side had high spawning fractions. In contrast, fish taken from the port-of-landing of North Haven in February, were mostly at Stage 5, producing the lowest estimate of spawning fraction of 0.18 for this region. The regional average of weighted estimates of spawning fraction was 0.5.

Southern Gulf St. Vincent

From the 14th January to 17th February 2020, there were six samples of Snapper collected from SGSV (south of 35°S), one from MFA 43 from the port-of-landing of West Beach and five from MFA 44 from the port-of-landing of Cape Jervis. They involved a total of 297 fish, which included 135 females. On each occasion, all females were classified as mature, with most at Stage 4 and a few at Stage 5. The estimates of spawning fraction ranged from 0.54 to 0.97, with no obvious temporal pattern to the variation (Table 2.4). The regional average of the weighted estimates of spawning fraction was 0.82.

Table 2.4. Summary of results on reproductive biology from adult Snapper sampled throughout the summer of 2019/20. For each region, the results show the location where fishing occurred (or port-of-landing from which the fishing operation took place). Also shown are the numbers of females at the different macroscopic stages of reproductive development, the numbers that were mature and spawning from which the spawning fractions were calculated.

Gulf	**Region**	**Location (Port of Landing)**	**Date**	**Number females**	**Number mature females**	**Number not spawning**	**Number spawning**	**Unweighted spawning fraction**	**Weighting**	**Weighted spawning fraction**
Spencer Gulf	NSG	(Port Pirie)	05-Dec-19	15	15	15	0	0		
Spencer Gulf	NSG	(Port Pirie)	12-Dec-19	34	34	34	0	0		
Spencer Gulf	NSG	Santa Anna	5-Dec-19	15	15	?	at least 6	at least 0.4		
Spencer Gulf	NSG	Santa Anna	7-Dec-19	3	3	?	at least 1	at least 0.33		
Spencer Gulf	NSG	The Illusion	6-Dec-19	5	5	1	4	0.8		
Spencer Gulf	NSG	Estelle Star	08-Dec-19	21	21	?	at least 6	at least 0.29		
Spencer Gulf	NSG	Estelle Star	11-Dec-19	72	72	?	at least 16	at least 0.22		
Spencer Gulf	NSG	(Port Broughton)	18-Dec-19	21	21	?	at least 3	at least 0.14		
Spencer Gulf	SSG	(Port Victoria)	10-Feb-20	20	20	9	11	0.55	1.03	0.57
Spencer Gulf	SSG	(Port Victoria)	13-Feb-20	6	6	5	1	0.17	0.31	0.05
Spencer Gulf	SSG	(Port Victoria)	17-Feb-20	22	22	16	6	0.27	1.13	0.31
Spencer Gulf	SSG	(Port Victoria)	23-Feb-20	15	15	7	8	0.53	0.77	0.41
Spencer Gulf	SSG	(Port Victoria)	24-Feb-20	18	18	17	1	0.06	0.93	0.05
Spencer Gulf	SSG	(Port Victoria)	29-Feb-20	31	31	17	14	0.45	1.60	0.72
Spencer Gulf	SSG	(Port Victoria)	11-Mar-20	24	24	18	6	0.25	1.24	0.31
Gulf St. Vincent	NGSV	Stansbury	17-Jan-20	22	22	10	12	0.55	1.06	0.58
Gulf St. Vincent	NGSV	Stansbury	18-Jan-20	14	14	3	11	0.79	0.67	0.53
Gulf St. Vincent	NGSV	Stansbury	04-Feb-20	32	31	19	12	0.39	1.49	0.58
Gulf St. Vincent	NGSV	Black Point/ Port Julia	18-Jan-20	5	5	0	5	1.0	0.24	0.24
Gulf St. Vincent	NGSV	Black Point/ *Zanoni*	21-Jan-20	31	31	12	19	0.61	1.49	0.91
Gulf St. Vincent	NGSV	Northhaven	10-Feb-20	22	22	18	4	0.18	1.06	0.19
Gulf St. Vincent	SGSV	MFA 44 – (Cape Jervis)	14-Jan-20	29	29	1	28	0.97	1.29	1.24
Gulf St. Vincent	SGSV	MFA 44 – (Cape Jervis)	16-Jan-20	29	29	1	28	0.97	1.29	1.24
Gulf St. Vincent	SGSV	MFA 43 – (West Beach)	29-Jan-20	28	28	12	16	0.57	1.24	0.71
Gulf St. Vincent	SGSV	MFA 44 – (Cape Jervis)	7-Feb-20	20	20	3	17	0.85	0.89	0.76
Gulf St. Vincent	SGSV	MFA 44 – (Cape Jervis)	11-Feb-20	13	13	6	7	0.54	0.58	0.31
Gulf St. Vincent	SGSV	MFA 44 – (Cape Jervis)	17-Feb-20	16	16	1	15	0.94	0.71	0.67

2.3.2 Estimates of reproductive parameters for 2021/22

Spencer Gulf

From the 11th to 17th December 2021, samples of Snapper were collected from Spencer Gulf. Most were taken in NSG (north of 34°S), with only four taken from SSG (Fig. 2.3). As such, the samples were considered as coming from three zones: a northern zone with fishing done from the port-of-landing of Port Pirie; a mid-zone from the port-of-landing of Port Broughton; and a southern zone with fishing from the port-of-landing of Wallaroo. In total, there were 503 Snapper sampled that included 266 females.

Of the 100 females collected from north of Port Pirie only five fish from one sample were assessed to be spawning. The estimated spawning fraction of this sample was 0.31, whilst the estimates for the other samples were zero (Table 2.5). The average of the weighted estimates of spawning fraction for this zone is 0.05. The samples from the mid-zone came from places such as The Illusion, the Santa Anna, and Plank Beacon. These samples were dominated by spawning fish and the estimates of spawning fraction ranged from 0.64 to 1.0. The average of the weighted estimates of spawning fraction was 0.81. For the southern zone, eight places were sampled between 15th and 17th December 2021. These were located offshore from Wallaroo and extended south to a line across the gulf from Port Neill to Port Hughes. They provided a total of 147 Snapper of which 67 were females. For several samples, the estimates of spawning fraction were very high, ranging from 0.75 to 1.0. However, at the Estelle Star, the females were dominated by those at Stage 2, so the spawning fractions were very low. Another locality, (sample code – WA12/2109) also produced a low estimate of spawning fraction. The average of the weighted estimates of spawning fraction for this region was 0.83.

Northern Gulf St. Vincent

For Gulf St. Vincent, a total of 20 localities were sampled for adult Snapper between the 7th and 15th January 2022 (Fig. 2.3). For NGSV, i.e., those localities that were located north of 34°S, there were 264 fish sampled from 10 localities that included 119 females. For those females captured off Stansbury the spawning fractions were 1.0 (Table 2.5). For the samples collected from further north, the spawning fractions were also high, generally exceeding 0.75. For several samples the lower estimates of spawning fraction related to high proportions of females that were classified to Stage 5. So, this was a transition period with females approaching the end of their spawning seasons. The average of the weighted estimates of spawning fraction for this region was 0.83.

Southern Gulf St. Vincent

For SGSV, there were also 10 localities sampled between 11th and 15th January (Fig. 2.3). They produced 216 Snapper which included 91 females. For those captured off the metropolitan coastline down to Cape Jervis, the spawning fractions were very high, generally >0.8 (Table 2.5). Few females were classified to Stage 5. In comparison, for the 10 females that were sampled in the vicinity of southern Yorke Peninsula, six were at Stage 5 and only one was spawning. As such, these produced low estimates of spawning fraction. Overall, the average of the weighted estimates of spawning fractions was 0.84.

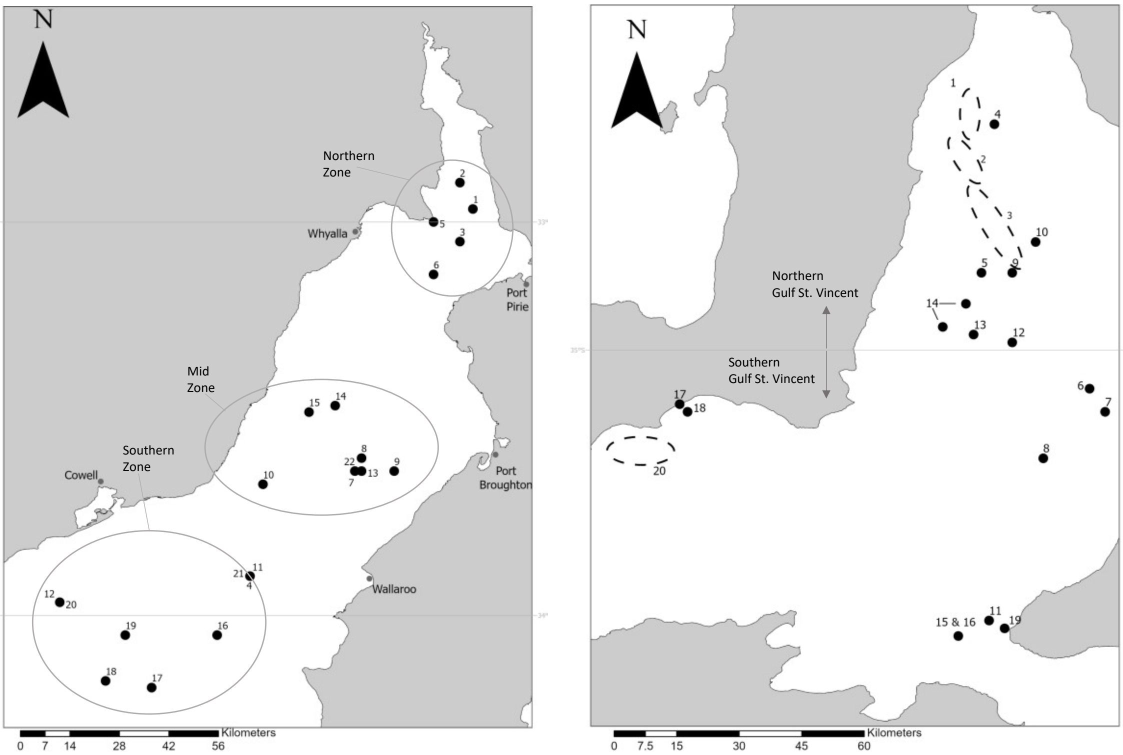


Fig. 2.3. Maps of the regions where sampling of adult Snapper was done in 2021/22. Left – the northern part of Spencer Gulf showing the Northern Zone, Mid Zone and Southern Zone, as differentiated in the text. Right – Gulf St. Vincent and Investigator Strait showing the latitudinal division between Northern Gulf St. Vincent and Southern Gulf St. Vincent. The sample locations are indicated as numbered dots or as hatched areas.

Table 2.5. Summary of results on reproductive biology from adult Snapper sampled throughout the summer of 2021/22. For each region, the results show the location where fishing occurred (or port-of-landing from which the fishing operation took place). Also shown are the numbers of females at the different macroscopic stages of reproductive development, the numbers that were mature and spawning from which the spawning fractions were calculated.

Gulf	Zone or Region	Location (Port of Landing)	Sample code	Date	Number females	Number mature females	Number not spawning	Number spawning	Unweighted spawning fraction	Weighting	Weighted spawning fraction
Spencer Gulf	North	(Port Pirie)	PP12/2101	11-Dec-21	52	52	52	0	0.00	2.48	0.00
Spencer Gulf	North	(Port Pirie)	PP12/2102	11-Dec-21	16	16	11	5	0.31	0.76	0.24
Spencer Gulf	North	(Port Pirie)	PP12/2103	11-Dec-21	7	7	7	0	0.00	0.33	0.00
Spencer Gulf	North	(Port Pirie)	PP12/2104	12-Dec-21	17	17	17	0	0.00	0.81	0.00
Spencer Gulf	North	(Port Pirie)	PP12/2105	12-Dec-21	13	13	13	0	0.00	0.62	0.00
Spencer Gulf	Mid	(Port Broughton)	MB12/2101	17-Dec-21	8	8	1	7	0.88	0.79	0.69
Spencer Gulf	Mid	(Port Broughton)	PB12/2101	16-Dec-21	16	16	5	11	0.69	1.58	1.09
Spencer Gulf	Mid	(Port Broughton)	PB12/2102	16-Dec-21	7	7	1	6	0.86	0.69	0.59
Spencer Gulf	Mid	(Port Broughton)	PB12/2103	16-Dec-21	14	14	5	9	0.64	1.38	0.89
Spencer Gulf	Mid	(Port Broughton)	WA12/2101	14-Dec-21	12	12	1	11	0.92	1.19	1.09
Spencer Gulf	Mid	(Port Broughton)	WA12/2102	14-Dec-21	14	14	2	12	0.86	1.38	1.19
Spencer Gulf	Mid	(Port Broughton)	WA12/2103	14-Dec-21	5	5	0	5	1.00	0.49	0.49
Spencer Gulf	Mid	(Port Broughton)	WA12/2104	15-Dec-21	5	5	0	5	1.00	0.49	0.49
Spencer Gulf	South	Estelle Star	ES12/2101	15-Dec-21	10	10	10	0	0.00	1.14	0.00
Spencer Gulf	South	Estelle Star	ES12/2102	16-Dec-21	9	9	8	1	0.11	1.03	0.11
Spencer Gulf	South	Jurassic Park	JP12/2101	11-Dec-21	8	8	1	7	0.88	0.91	0.80
Spencer Gulf	South	Jurassic Park	JP12/2102	17-Dec-21	11	11	0	11	1.00	1.25	1.25
Spencer Gulf	South	Mountain	MT12/2101	16-Dec-21	12	12	5	7	0.58	1.37	0.80
Spencer Gulf	South	(Wallaroo)	WA12/2106	15-Dec-21	8	8	2	6	0.75	0.91	0.68
Spencer Gulf	South	(Wallaroo)	WA12/2107	16-Dec-21	13	12	3	9	0.75	1.37	1.03
Spencer Gulf	South	(Wallaroo)	WA12/2108	16-Dec-21	5	5	0	5	1.00	0.57	0.57
Spencer Gulf	South	(Wallaroo)	WA12/2109	17-Dec-21	4	4	3	1	0.25	0.46	0.11
Gulf St. Vincent	NGSV	(Ardrossan)	AR01/2201	07-Jan-22	21	21	4	17	0.81	1.89	1.53
Gulf St. Vincent	NGSV	(Ardrossan)	AR01/2202	08-Jan-22	14	14	3	11	0.79	1.26	0.99
Gulf St. Vincent	NGSV	(Ardrossan)	AR01/2203	09-Jan-22	22	22	5	17	0.77	1.98	1.53
Gulf St. Vincent	NGSV	(Ardrossan)	AR01/2204	09-Jan-22	3	3	2	1	0.33	0.27	0.09
Gulf St. Vincent	NGSV	(North Haven)	NH01/2201	11-Jan-22	14	14	1	13	0.93	1.26	1.17
Gulf St. Vincent	NGSV	(North Haven)	NH01/2202	11-Jan-22	7	7	3	4	0.57	0.63	0.36
Gulf St. Vincent	NGSV	(North Haven)	NH01/2203	12-Jan-22	8	8	1	7	0.88	0.72	0.63
Gulf St. Vincent	NGSV	Stansbury	ST01/2201	09-Jan-22	3	3	0	3	1.00	0.27	0.27
Gulf St. Vincent	NGSV	Stansbury	ST01/2202	12-Jan-22	7	7	0	7	1.00	0.63	0.63
Gulf St. Vincent	NGSV	Stansbury	St01/2203	12-Jan-22	12	12	0	12	1.00	1.08	1.08
Gulf St. Vincent	SGSV	(Cape Jervis)	CJ01/2201	11-Jan-22	24	24	3	21	0.88	2.64	2.31
Gulf St. Vincent	SGSV	(Cape Jervis)	CJ01/2202	13-Jan-22	19	19	0	19	1.00	2.09	2.09
Gulf St. Vincent	SGSV	(Cape Jervis)	CJ01/2203	13-Jan-22	6	6	1	5	0.83	0.66	0.55
Gulf St. Vincent	SGSV	(Cape Jervis)	CJ01/2204	14-Jan-22	2	2	0	2	1.00	0.22	0.22
Gulf St. Vincent	SGSV	(Foul Bay)	FO01/2201	15-Jan-22	1	1	0	1	1.00	0.11	0.11

Gulf St. Vincent	SGSV	(Foul Bay)	FO01/2202	14-Jan-22	2	2	2	0	0.00	0.22	0.00
Gulf St. Vincent	SGSV	(Foul Bay)	FO01/2203	14-Jan-22	7	7	7	0	0.00	0.77	0.00
Gulf St. Vincent	SGSV	(North Haven)	NH01/2204	10-Jan-22	17	17	1	16	0.94	1.87	1.76
Gulf St. Vincent	SGSV	(North Haven)	NH01/2205	10-Jan-22	5	5	1	4	0.80	0.55	0.44
Gulf St. Vincent	SGSV	(North Haven)	NH01/2206	10-Jan-22	8	8	0	8	1.00	0.88	0.88

2.3.3 Estimates of reproductive parameters for 2005/06, 2006/07 and 2007/08

Between 2005 and 2008, only NSG was considered (Saunders 2009, Saunders et al. 2012). Samples of adult Snapper were obtained from the commercial and charter boat sectors and by research sampling. Sampling effort was concentrated in December and January of each summer, but sampling did occur in other months including November and February. All samples were pooled for the region, so there was no specific information reported for port-of-landing or fishing location. There were some samples collected before and after those reported, but because they did not involve spawning fish, they are not included in Table 2.6.

For the summer of 2005/06, the period during which spawning fish were detected was from 24th November 2005 until 6th January 2006, with no evidence of spawning in February 2006. The estimates of spawning fraction were generally very high but ranged from 0 to 0.89 (Table 2.6). Such high estimates relate to individual fish spawning, on average, nearly every day. Nevertheless, low estimates of spawning fraction were obtained on the 3rd, 9th, and 22nd December 2005.

For the summer of 2006/07, spawning fish were detected throughout the two-months from late November until late January, (i.e., marginally longer than during the previous year) (Table 2.6). No spawning fish were detected in February or later. For each sample considered from throughout both December and January, the estimates of spawning fraction generally exceeded 0.5, and were often considerably higher. Only for two samples taken on 10th and 19th January 2007 were low estimates attained.

For 2007/08, the first evidence of spawning was collected on the 4th December 2007 and the last sample with spawning fish was on 11th January 2008 (Table 2.6). The estimates of spawning fraction ranged from 0 to 0.73, and were, in general, considerably lower than those obtained during the previous two summers. This suggests inter-annual variation in spawning fraction for this region.

Table 2.6. Summary of results on reproductive biology from adult Snapper sampled from throughout Northern Spencer Gulf during the summers of 2005/06, 2006/07 and 2007/08. Information on where fishing occurred was not provided. Data shown are the numbers of mature females, those that were spawning and the estimated spawning fractions. Blanks indicate that sample sizes were too low to estimate spawning fraction.

Region	**Location (Port of Landing)**	**Date**	**Number females**	**Number mature females**	**Number spawning**	**Spawning fraction**
NSG		24-Nov-05		7	1	0.14
NSG		01-Dec-05		18	16	0.89
NSG		02-Dec-05		10	9	0.9
NSG		03-Dec-05		9	5	0.56
NSG		04-Dec-05		5	3	0.6
NSG		07-Dec-05		3	2	
NSG		08-Dec-05		3	1	
NSG		09-Dec-05		6	2	0.33
NSG		11-Dec-05		6	4	0.67
NSG		13-Dec-05		6	5	0.83
NSG		14-Dec-05		54	47	0.87
NSG		16-Dec-05		31	20	0.65
NSG		18-Dec-05		4	2	
NSG		19-Dec-05		2	1	
NSG		21-Dec-05		9	8	0.89
NSG		22-Dec-05		4	0	0
NSG		28-Dec-05		7	5	0.71
NSG		30-Dec-05		5	3	0.6
NSG		4-Jan-06		7	6	0.86
NSG		6-Jan-06		13	11	0.85
NSG		28-Nov-06		11	4	0.36
NSG		01-Dec-06		14	10	0.71
NSG		05-Dec-06		17	10	0.59
NSG		06-Dec-06		4	3	
NSG		08-Dec-06		10	6	0.6
NSG		12-Dec-06		4	4	1.0
NSG		13-Dec-06		19	11	0.58
NSG		14-Dec-06		7	7	1.0
NSG		17-Dec-06		18	15	0.83
NSG		18-Dec-06		6	3	0.5
NSG		21-Dec-06		10	10	1.0
NSG		27-Dec-06		11	11	1.0
NSG		28-Dec-06		8	7	0.88
NSG		29-Dec-06		21	14	0.67
NSG		03-Jan-07		3	1	
NSG		05-Jan-07		9	7	0.78
NSG		10-Jan-07		7	1	0.14
NSG		12-Jan-07		9	7	0.78
NSG		17-Jan-07		8	8	1.0
NSG		19-Jan-07		9	2	0.22
NSG		23-Jan-07		9	7	0.78
NSG		04-Dec-07		18	3	0.17
NSG		07-Dec-07		10	5	0.5
NSG		12-Dec-07		11	8	0.73
NSG		21-Dec-07		6	0	0
NSG		28-Dec-07		7	4	0.57
NSG		31-Dec-07		2	1	
NSG		09-Jan-08		8	1	0.13
NSG		11-Jan--08		6	2	0.33

2.3.4 Estimates of reproductive parameters for 2000-2002

From November 2000 until February 2002, numerous samples of Snapper were collected from throughout NSG (Fig 2.1). Through that period the State-wide catches were dominated by those from NSG and SSG, whilst there was high biomass of Snapper throughout Spencer Gulf (Fowler et al. 2016, Fowler et al. 2020). This adult sampling that provided information on reproductive biology was undertaken to contribute to an application of the DEPM (Fowler unpublished). Through the months of spring, summer and early autumn across these years, a total of 1,350 Snapper were processed, which included 708 females (Table 2.7).

Across the three summers, eight samples of Snapper were collected from fishing operations that operated out of Port Pirie as the port-of-landing (Table 2.7). More specific spatial information is not available except that fishing was done in MFA 21, including at Musgrave Shoal. Across the three summers, the timing of fishing events ranged from early November until mid-April. A total of 397 fish were sampled that included 211 females. Generally, these samples were characterised by the lack of evidence for spawning activity. Most females were classified to Stages 1, 2 and 5, a few to Stage 3, whilst none were classified to Stage 4. As such, although most females were mature, the lack of evidence for spawning generally resulted in estimates of spawning fraction of zero. Two samples were collected from Whyalla as the port-of-landing late in the reproductive season of 1999/00. Both had spawning fractions of zero. In contrast, in mid-December 2000, there were two small samples from the wreck of the *Leeton* that were obtained by fishing from the MRV *Ngerin*. The ovaries from all seven females were at Stage 4, resulting in estimates of spawning fraction of 1.0 for both samples.

Numerous samples were collected between February 2000 and February 2002 from Wallaroo and Port Broughton as the ports-of-landing (Table 2.7). The specific locations where fishing occurred are not known but ranged across the gulf between the eastern and western shorelines. Whilst those samples collected in November, February or March had spawning fractions of zero or low values, those taken during December 2000 were generally high, ranging from 0.63 to 0.77. These data show evidence of spawning in NSG in early November, a high rate of spawning activity during December, but no spawning in February or March.

In addition to the samples that were collected from Wallaroo and Port Broughton as the ports-of-landing, there were also seven samples of Snapper that were captured and processed from the wreck of The Illusion. The first two samples were captured in April 2000, which included no spawning females. Then, there were three samples collected in mid-December 2000. For these, all fish were mature of which most were spawning, producing estimates of spawning fraction that ranged from 0.5 to 0.93 (Table 2.7). The final sample collected from The Illusion in late November 2001 included a relatively high proportion of spawning fish, with an estimate of spawning fraction of 0.63.

Table 2.7. Summary of results on reproductive biology from adult Snapper sampled from throughout Northern Spencer Gulf during the summers of 2000/01, 2001/02 and 2002/03. The results show the location where fishing occurred (or port-of-landing from which the fishing operation took place). Also shown are the numbers of females the different macroscopic stages of reproductive development, the numbers that were mature and spawning, from which the spawning fractions were calculated.

Region	Location (Port of Landing)	Date	Number females	Number mature females	Number spawning	Spawning fraction
NSG	(Port Pirie)	27-Nov-00	14	4	0	0
NSG	(Port Pirie)	14-Dec-00	26	3	0	0
NSG	(Port Pirie)	9-Apr-01	9	9	0	0
NSG	(Port Pirie)	3-Nov-01	45	45	possible 9	?
NSG	(Port Pirie)	06-Dec-01	26	26	0	0
NSG	(Port Pirie)	15-Feb-02	41	41	0	0
NSG	(Port Pirie)	17-Mar-02	26	12	0	0
NSG	(Port Pirie)	16-Apr-02	24	24	0	0
NSG	(Whyalla)	21-Feb-00	14	12	0	0
NSG	(Whyalla)	21-Apr-00	122	119	0	0
NSG	*Leeton* wreck	15-Dec-00	4	4	4	1.0
NSG	*Leeton* wreck	16-Dec-00	3	3	3	1.0
NSG	(Wallaroo)	01-Feb-00	13	0	0	0
NSG	(Wallaroo)	04-Feb-00	29	29	0	0
NSG	(Wallaroo)	04-Nov-00	7	7	at least 1	at least 0.14
NSG	(Wallaroo)	06-Nov-00	8	8	at least 3	at least 0.375
NSG	(Wallaroo)	08-Dec-00	36	23	4	0.17
NSG	(Wallaroo)	12-Dec-00	15	15	10	0.67
NSG	(Wallaroo)	15-Dec-00	16	16	10	0.63
NSG	(Wallaroo)	16-Dec-00	17	17	13	0.77
NSG	(Port Broughton)	14-Dec-00	7	6	0	0
NSG	(Port Broughton)	14-Dec-00	6	6	4	0.67
NSG	(Port Broughton)	15-Dec-00	14	14	10	0.71
NSG	(Wallaroo)	14-Mar-01	26	26	0	0
NSG	(Wallaroo)	22-Nov-01	11	11	8	0.72
NSG	(Wallaroo)	13-Feb-02	10	10	0	0
NSG	The Illusion	11-Apr-00	14	10	0	0
NSG	The Illusion	13-Apr-00	9	9	0	0
NSG	The Illusion	12-Dec-00	15	15	14	0.93
NSG	The Illusion	13-Dec-00	6	6	3	0.5
NSG	The Illusion	14-Dec-00	11	11	9	0.82
NSG	The Illusion	20-23-Nov-01	84	84	53	0.63

2.3.5 Estimates of reproductive parameters for 1994-1996

In the summer months of 1994/95 and 1995/96, a total of 21 samples of adult Snapper were sampled from throughout NSG. They were collected as part of the first attempt to apply the DEPM to estimate the spawning biomass of Snapper in one region in South Australia (McGlennon 2003). Over the two summers the samples were concentrated in the middle of each of November, December and January. Apart from one sample that came from Eastern Shoal, no specific information is available on the fishing location, as the samples were generally related to a port-of-landing. These were divisible into three approximate latitudinal zones, a northern, a mid and a southern zone.

For the Northern Zone around Port Pirie and Whyalla, six samples were collected between 11th November 1994 and 17th January 1996 that included 91 females, of which only seven were classified as spawning at the time of capture (Table 2.8). As such, the resulting estimates of spawning fraction were generally very low ranging from 0 to 0.25.

There were eight samples from the Mid-Zone whose collection date ranged from 12th November 1994 until 18th January 1996. They involved a total of 160 females. One or some spawning fish were identified from six of the eight samples, which covered the date range from mid-November to mid-January (Table 2.8). There was considerable temporal variability in the estimates of spawning fraction, which were generally relatively low at <0.45, but ranged from 0 to 0.7. There appeared to be no pattern to this temporal variability, suggesting that the estimates may have related to where the samples were collected.

The samples from the Southern Zone were primarily taken in December 1995 and January 1996. There were 94 females captured from Cowell, Mitchellville, or Middle Bank. These samples included high proportions of spawning females, which produced the highest estimates of spawning fraction that ranged from 0.67 to 1.0 (Table 2.8).

Table 2.8. Summary of results on reproductive biology from adult Snapper sampled from throughout Northern Spencer Gulf during the summers of 1994, 1995 and 1996. The results show the location where fishing occurred or port-of-landing for the fishing operation. Also shown are the numbers of females, the numbers that were mature, those spawning and the resulting estimates of spawning fraction.

Zone	Location (Port of Landing)	Date	Number females	Number mature females	Number spawning	Spawning fraction
Northern	(Port Pirie)	11-Nov-94	4	4	1	0.25
Northern	(Port Pirie)	16-Dec-94	7	3	0	0
Northern	(Whyalla)	12-Nov-94	22	22	1	0.05
Northern	Eastern Shoal	14-15-Dec-95	25	25	1	0.04
Northern	(Whyalla)	14-Jan-96	13	13	0	0.04
Northern	(Port Pirie)	17-Jan-96	20	20	4	0.2
Mid	(Murninnie)	12-Nov-94	10	10	7	0.7
Mid	(Murninnie)	14-Dec-94	18	17	4	0.4
Mid	(Murninnie)	15-Dec-94	12	12	5	0.39
Mid	(Wood Point)	14-Dec-95	20	20	0	0
Mid	(Murninnie)	15-Jan-96	24	24	0	0
Mid	(Murninnie)	16-Jan-96	39	39	1	0.03
Mid	(Murninnie)	17-Jan-96	27	27	12	0.44
Mid	(Murninnie)	18-Jan-96	10	10	1	0.1
Southern	(Cowell)	16-Dec-94	14	14	13	0.93
Southern	(Mitchellville)	13-Dec-95	19	19	19	1.0
Southern	Middle Bank	13-Dec-95	16	16	11	0.69
Southern	(Mitchellville)	15-Jan-96	11	11	10	0.91
Southern	(Mitchellville)	15-Jan-96	21	21	21	1.0
Southern	(Mitchellville)	17-Jan-96	4	4	4	1.0
Southern	(Mitchellville)	17-Jan-96	9	6	6	0.67

2.4 Discussion

2.4.1 Within-region variability in spawning fractions for NSG

The five studies considered here that were done over the past 30 years or so provided results that were informative about the spatial and temporal aspects of the reproductive biology of Snapper in South Australia. Each study presented results for the region of NSG. Throughout the 1990s and early 2000s, the focus on this region reflects that the fishery was concentrated there, as it supported the highest level of fishable biomass. This, nevertheless, changed dramatically through the latter 2000s (Fowler et al. 2020). The results across studies indicated that in NSG, whilst spawning did occur in November, the highest levels of spawning fraction were generally attained through December and January. Furthermore, several studies indicated that by February, spawning in this region had finished for the season. This established a general pattern, i.e., increase in spawning fraction early in the season during November and early December, high levels during mid-season throughout December and early January, and then a quick drop to zero by February.

The studies done in NSG also informed about two other levels of variability in the estimates of spawning fraction. Firstly, even through December and January, when the spawning activity of Snapper was at its highest, there was considerable variation amongst different samples in the estimates of spawning fraction, even when taken around similar times. For example, for four samples of Snapper collected between 5th and 17th January 2007, the consecutive estimates of spawning fraction were 0.78, 0.14, 0.78 and 1.0. Similarly, three samples collected from Murninnie on the three consecutive days of 16-18th January 1996 produced estimates of spawning fraction of 0.03, 0.44 and 0.1, respectively. The differences between these estimates of spawning fraction are around an order of magnitude or more. Yet, the basis of this small-scale temporal variation is not understood despite the iteroparous nature of the species and the ability for individuals to spawn over consecutive days. It may well relate to the second observation regarding variation in estimates of spawning fraction, i.e., spatial differences in the estimates. Regardless of the timing, the samples that were collected in the northern part of NSG, i.e., predominantly from the ports-of-landing of Port Pirie and Whyalla, produced estimates of spawning fraction that were consistently low. Few 'spawning' fish were ever detected from this zone. These fish were generally classified to Stage 2, i.e., the maturation of oocytes had commenced, but few ovaries were ever classified to Stages 3 or 4, which indicated that the oocytes had not proceeded through to vitellogenesis. In contrast, the samples that involved high proportions of spawning fish, generally came from deeper, offshore waters such as the wreck of The Illusion. Overall, such spatial data indicate that there is clearly a within-region, spatial component to the variable estimates of spawning fraction. Such spatial variation suggests that habitat has an exogenous influence on the physiological processes of reproductive maturation. A similar phenomenon has been described for King George whiting (*Sillaginodes punctatus*), for which the spatial differences in reproductive biology are manifested at a regional scale, i.e., between the northern and southern regions of Spencer Gulf and Gulf St. Vincent (Fowler et al. 2000).

For the early studies on reproductive biology undertaken in NSG there was a lack of fine-scale spatial information about the places from where the samples of Snapper were collected. Only for some samples, primarily those collected on research cruises, was accurate information available for sample location. When samples were provided by representatives of the fishing sectors, often the only spatial information provided was the port-of-landing, with no specific information on place-of-capture or habitat. The consequence of this is that when several samples were considered from a port-of-landing or from the whole region that were sampled in a short time-period, this does not mean that the samples were taken from the same place or habitat. As such, the fine-scale temporal variability in estimates of spawning fractions discussed above, may well relate to spatial variability, i.e., different places and habitats being sampled on different days. Therefore, in the absence of precise spatial information from where samples of Snapper were collected, there is considerable confounding of the spatial and temporal influences on the estimates of reproductive parameters, including spawning fraction.

2.4.2 Regional variation in estimates of spawning fractions

The sampling undertaken in 2019/20 and 2021/22 was done in four different regions. In each year there were differences in when the samples were collected in the different regions. Nevertheless, the data indicated that there were regional differences in the durations of the seasons through which spawning occurred. As discussed above, two earlier studies for NSG indicated a spawning season of November to January. For NGSV in 2020, there was evidence that spawning continued until at least the 10th February and for SGSV until at least the 17th February. Furthermore, for SSG, the last sample collected on the 11th March still included spawning fish. These observations contribute to the long-held suspicion that the duration of the spawning season in the southern gulfs is more protracted than in the northern gulfs.

It has previously been demonstrated for Snapper that the timing of reproduction varies with latitude (Sheaves 2006, Wakefield 2006). Throughout temperate regions, Snapper reproduction occurs during spring-summer, and in sub-tropical to tropical regions it occurs from late autumn through to early spring, generally with a peak in winter. Such variation in timing is a feature that is typical of the family Sparidae (Sheaves 2006). By virtue of the different spawning times, the production of most eggs and larvae occurs at relatively similar water temperature regimes, despite the differences in latitude. In so doing, the eggs and larvae of Snapper across the latitudinal range of their distribution are exposed to a much-reduced range of environmental conditions compared to those to which the adult fish are exposed (Chapter 3). This range for Snapper eggs is approximately 18-22°C (Chapter 3), which optimises their chance of survivorship from a physiological perspective.

The differences in spawning periods for Snapper in the regions of South Australia may reflect their different water temperature regimes. The heat budgets of the two gulfs are dominated by surface heat exchange that results in seasonal water temperature gradients up the gulfs, i.e., the northern gulfs experience warmer summer but colder winter temperatures than do the waters of the southern gulfs and continental shelf (Nunes Vaz and Lennon 1986, de Silva Samarasinghe and Lennon 1987). Because of the regional differences in water temperature regimes, the timing and duration for when the fish experience the optimal water temperatures for egg and larval survival will vary regionally.

The samples collected for SSG, NGSV, and SGSV also displayed the within-region variability described above for NSG. For example, the estimates of spawning fraction for SSG over the period of 10th February to 11th March 2020 ranged from 0.06 to 0.55, whilst for NGSV from 17th January until 10th February 2020 were from 0.16 to 1.0. As suggested above for NSG, such small-scale temporal differences of almost an order of magnitude, could well relate to spatial variability with respect to the particular places within regions where samples of Snapper were collected.

2.4.3 Implications

In South Australia, estimating the fishable biomass for Snapper has become a fundamental component of the stock assessment process (Fowler et al. 2019, Fowler et al. 2020, Drew et al. 2022). The method of choice to achieve this is the daily egg production method (DEPM), whose methods were refined for application to Snapper (Steer et al. 2017). The resulting estimates of fishable biomass from the DEPM depend on the accuracy of the estimates of parameters, including for spawning fraction. This study considered the estimates of spawning fraction that resulted from five different studies on reproductive biology for Snapper that were done over several decades. It identified several levels of variation in the reproductive biology of Snapper. First, there were regional differences in the duration of the spawning seasons. These were prolonged in the southern gulfs and thought to relate to water temperature regimes. Secondly, within each region, there was considerable small-scale variation in the estimates of spawning fraction amongst different samples. This was thought to, at least partly, involve a component of spatial variation that related to an effect of habitat on gonad maturation and spawning. This implies a confounding between the spatial and temporal influences over maturation and spawning activity. Our inability to dissociate spatial and temporal influences reflects the limitations in the data available. Limited numbers of samples have generally been collected, whilst until recently, there has been limited spatial information for particular samples. Reproductive samples have often been accessed opportunistically or sampling has been very limited in space and time, i.e., a few samples collected at limited places for short periods of time. Logistic issues restrict the capacity to sample broadly throughout a region particularly over the short period that corresponds to the plankton sampling program during DEPM sampling. This has impacted on the capacity to provide realistic and acceptable region-wide estimates of spawning fraction. Given the likely influence of habitat on reproductive biology, there is a challenge to collect sufficient samples from across a region to accurately represent the range in spawning fractions at that time, and to stratify the whole region according to the range in estimates of spawning fraction.

As indicated above, at this stage, the sampling programs to obtain reproductive information on Snapper have been limited. It has not been possible to sample repeatedly at the same location, to determine how estimates of spawning fraction change throughout a reproductive season. As such, it has clearly been impossible to undertake such sampling repeatedly at a number of different places simultaneously, in order to document the spatial variation in estimates that would otherwise contribute to resolving the confounding that occurs in space and time. It is likely that the most tractable way to undertake repeated sampling at particular places would be by sampling catches from the commercial sector. This would require fishers to be willing to provide accurate spatial information about their fishing activities. However, this will remain extremely challenging to achieve whilst spatial and seasonal fishery closures limit the opportunity for commercial fishing to occur throughout the spawning season.

2.5 References

De Silva Samarasinghe, J.R., Lennon, G.W. (1987). Hypersalinity, flushing and transient salt-wedges in a tidal gulf – an inverse estuary. Estuarine, Coastal and Shelf Science 24: 483-498.

Drew, M.J., Rogers, T.A., McGarvey, R., Feenstra, J., Matthews, D., Matthews, J., Earl, J., Smart, J., Noell, C., and Fowler, A.J. (2022). Snapper (*Chrysophrys auratus*) Stock Assessment Report 2022. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2007/000523-7. SARDI Research Report Series No. 1155. 178 pp.

Farley, J.H., Davis, T.L.O. (1998). Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*, in the Indian Ocean south of the Sunda Islands. Fishery Bulletin 96: 223-236.

Fowler, A.J., McLeay, L., Short, D.A. (1999). Reproductive mode and spawning information based on gonad analysis for the King George whiting (Percoidei: Sillaginidae) from South Australia. Marine and Freshwater Research 50: 1-4.

Fowler, A.J., McLeay, L., Short, D.A. (2000). Spatial variation in size and age structures and reproductive characteristics of the King George whiting (Percoidei: Sillaginidae) in South Australian waters. Marine and Freshwater Research 51: 11-22.

Fowler, A.J., McGarvey. R., Carroll, J., Feenstra, J.E., Jackson, W.B., Lloyd, M.T. (2016). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-4. SARDI Research Report Series No. 930. 82pp.

Fowler, A.J., Steer, M.A., McGarvey. R., Smart, J. (2019). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2019/000331-1. SARDI Research Report Series No. 1031. 62pp.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

Hunter, J.R., 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 66-77. US Dept Commerce, NOAA Technical Report NMFS 36.

Jackson, G., Cheng, Y. (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(2): 243-257.

Kailola, P., Williams, M.J., Stewart, P.C., Reichlet, R.E., McNee. A., Grieve. C. (1993). Australian fisheries resources. Bureau of Resource Sciences and Fisheries Research and Development Corporation, Canberra.

Lasker, R. (1985). An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*)). US Department of Commerce. NOAA Technical Report NMFS 36, 99 pp.

Matsuyama, M., Adachi, S., Nagahama, Y., Matsura, S. (1988). Diurnal rhythm of oocyte development and plasma steroid hormone levels in the females Red Sea Bream, *Pagrus major*, during the spawning season. Aquaculture 73: 357-372.

McGlennon, D. (2003). The fisheries biology and population dynamics of Snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. PhD. Thesis, University of Adelaide, Adelaide, South Australia. 212 pp.

Nunes, R.A., 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.

Pankhurst, N.W., Munday. P.L. (2011). Effects of climate change on fish reproduction and early life history stages. Marine and Freshwater Research 62: 1015-1026.

Pankhurst, N.W., Porter, M.J.R. (2003). Cold and dark or warm and light: variation on the theme of environmental control of reproduction. Fish Physiology and Biochemistry 28: 385-389.

Saunders, R.J. (2009). The reproductive biology and recruitment dynamics of Snapper, *Chrysophrys auratus*. PhD. Thesis, University of Adelaide, Adelaide, South Australia. 154 pp.

Saunders, R.J., Fowler, A.J., Gillanders, B.M. (2012). The spawning dynamics of snapper (*Chrysophrys auratus*) in northern Spencer Gulf, South Australia. New Zealand Journal of Marine and Freshwater Research 46: 491-510.

Scott, S.G., 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., 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.

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

Steer, M.A., McGarvey, R., Oxley, A., Fowler, A.J., Grammer, G., Ward, T.M., Westlake, E., Matthews, D., Matthews, J. Developing a fishery independent estimate of biomass for Snapper (*Chrysophrys auratus*). Final report to FRDC (Project No. 2014/019). 68pp.

Wakefield, C.B. (2010). Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. Journal of Fish Biology 77: 1359-1378.

Wallace, R.A., Selman, K. (1981). Cellular dynamic aspects of oocyte growth in teleosts. American Zoologist 21: 325-343.

Zeldis, J.R. (1993). Applicability of egg surveys for spawning-stock biomass estimation of Snapper, Orange Roughy, and Hoki in New Zealand. Bulleting of Marine Science 53(2): 864-890.

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

2.6 Appendices

2.6.1 Macroscopic appearance of ovaries

Stage 3 Ovaries

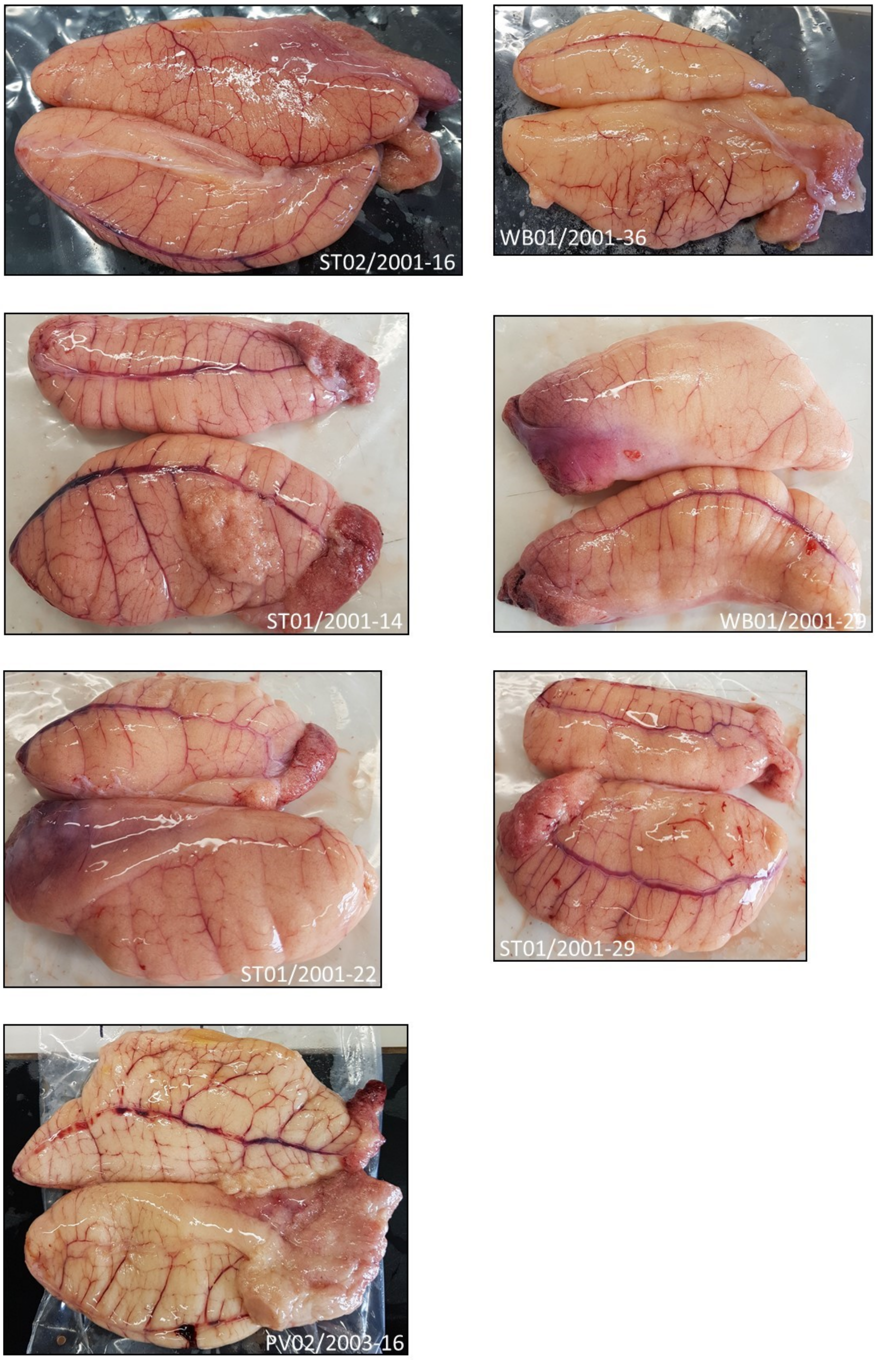


Fig. A2.1. Photographs of whole Snapper ovaries classified macroscopically to Stage 3. They were relatively large, yellow to orange to pink, with blood vessels ramifying across the surface. To the naked eye, individual oocytes were opaque.

Stage 4 Ovaries

Fig. A2.2. Photographs of whole Snapper ovaries classified macroscopically to Stage 4. Ovaries were heavier and darker than those at Stage 3 due to the uptake of fluid by the hydrating oocytes that became larger and translucent amongst the smaller opaque oocytes. The ovaries were less solid and more watery than for those at Stage 3. For ovary CE12/2005-33 ovulation had already occurred as the hydrated oocytes were accumulated at the anterior end of the ovary, ready to be spawned.

Stage 5 – Ovaries

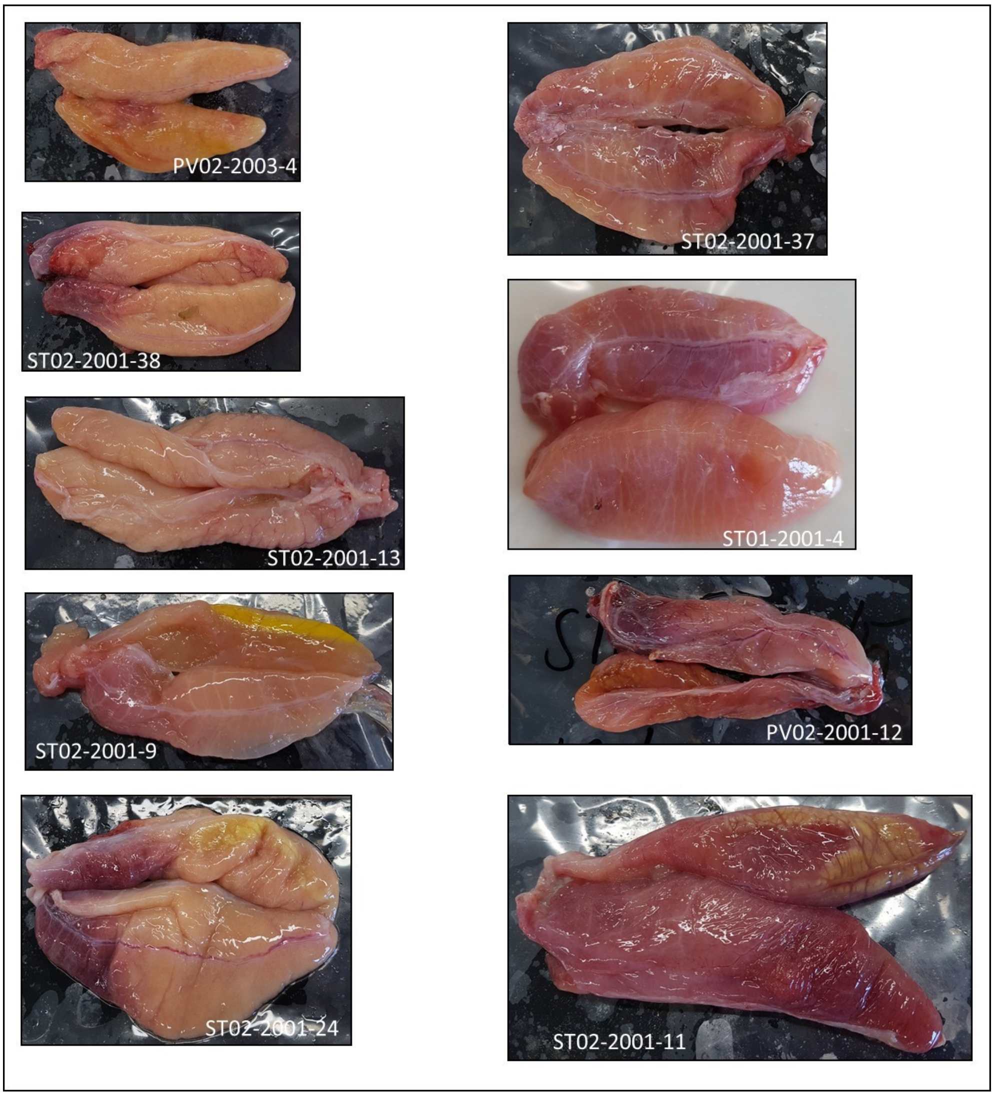


Fig. A2.3. Photographs of whole Snapper ovaries classified macroscopically to Stage 5. Ovaries are smaller than those at Stages 3 and 4, are flaccid, pink to dark pink, or yellow to brown. Individual oocytes cannot be discerned.

2.6.2 Relationship between macroscopic stage and microscopic characteristics

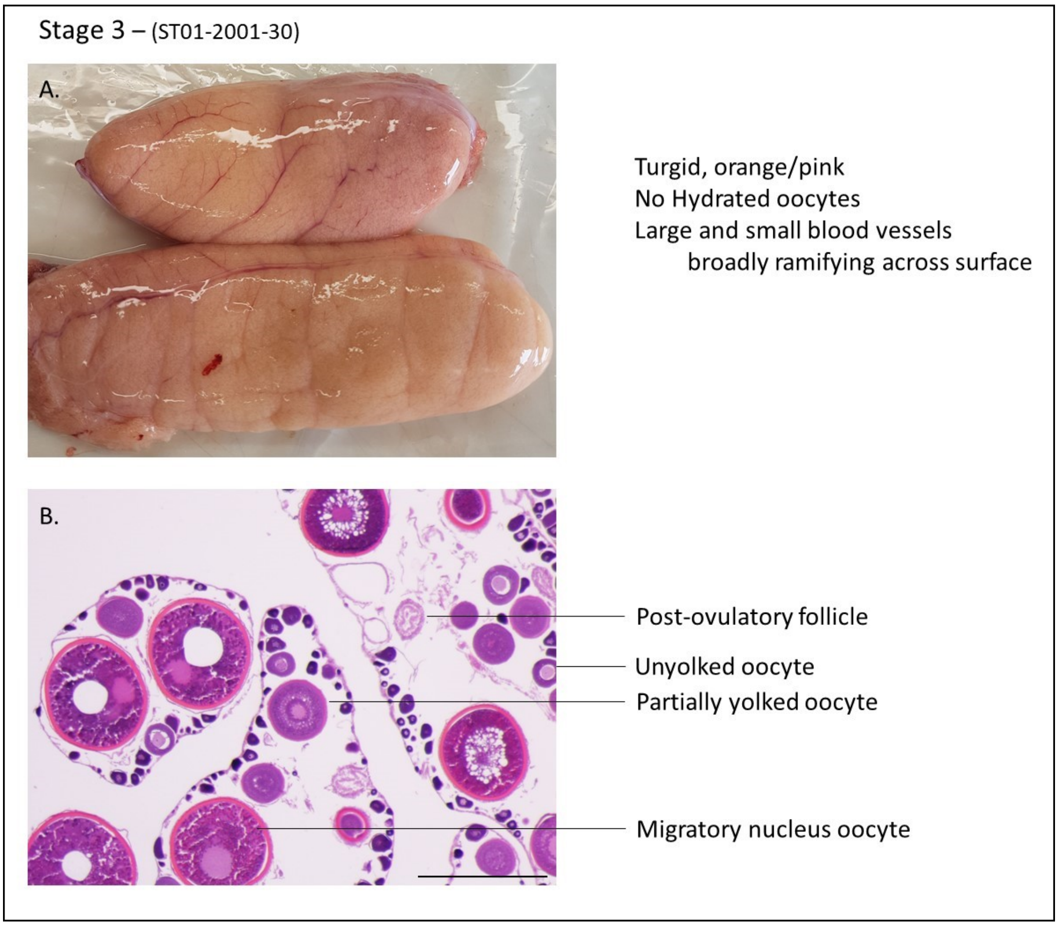


Fig. A2.4. Snapper – ST01/2001-30 (721 mm CFL, 5.71 kg). A. Photograph of whole ovaries. B. Photomicrograph of histological slide from one ovary. Scale bar = 500 µm.

- Ovary structure disrupted.
- Presence of degenerating post-ovulatory follicles indicate that spawning had occurred in the past day or so.
- Migratory nucleus oocytes indicate the start of the hydration process, such that spawning would have happened later on the day of capture.

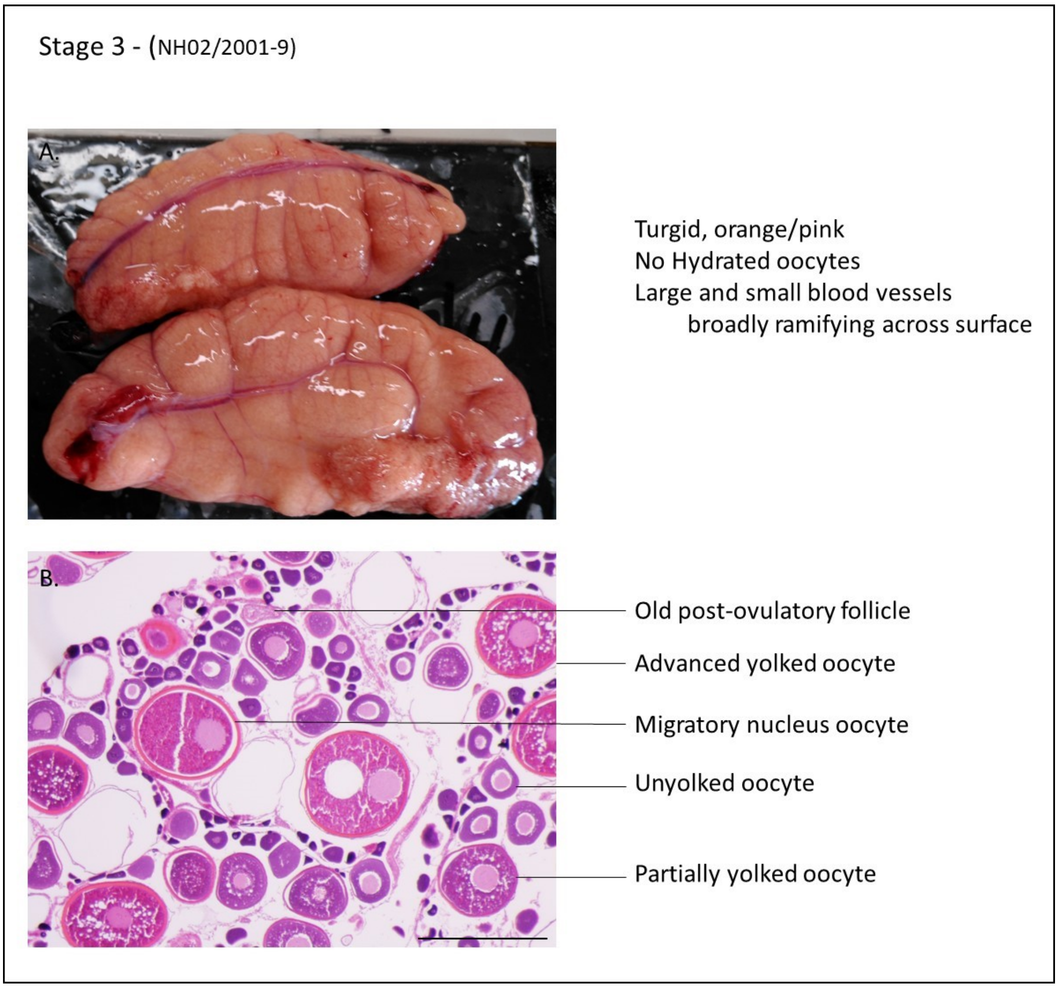


Fig. A2.5. Snapper – NH02/2001-9 (728 mm CFL, 6.05 kg). A. Photograph of whole ovaries. B. Photomicrograph of histological slide from one ovary. Scale bar = 500 µm.

- Presence of degenerating post-ovulatory follicles indicate that spawning had occurred in the past day or so.
- Migratory nucleus oocytes indicate the start of the hydration process, such that spawning would have happened later on the day of capture.

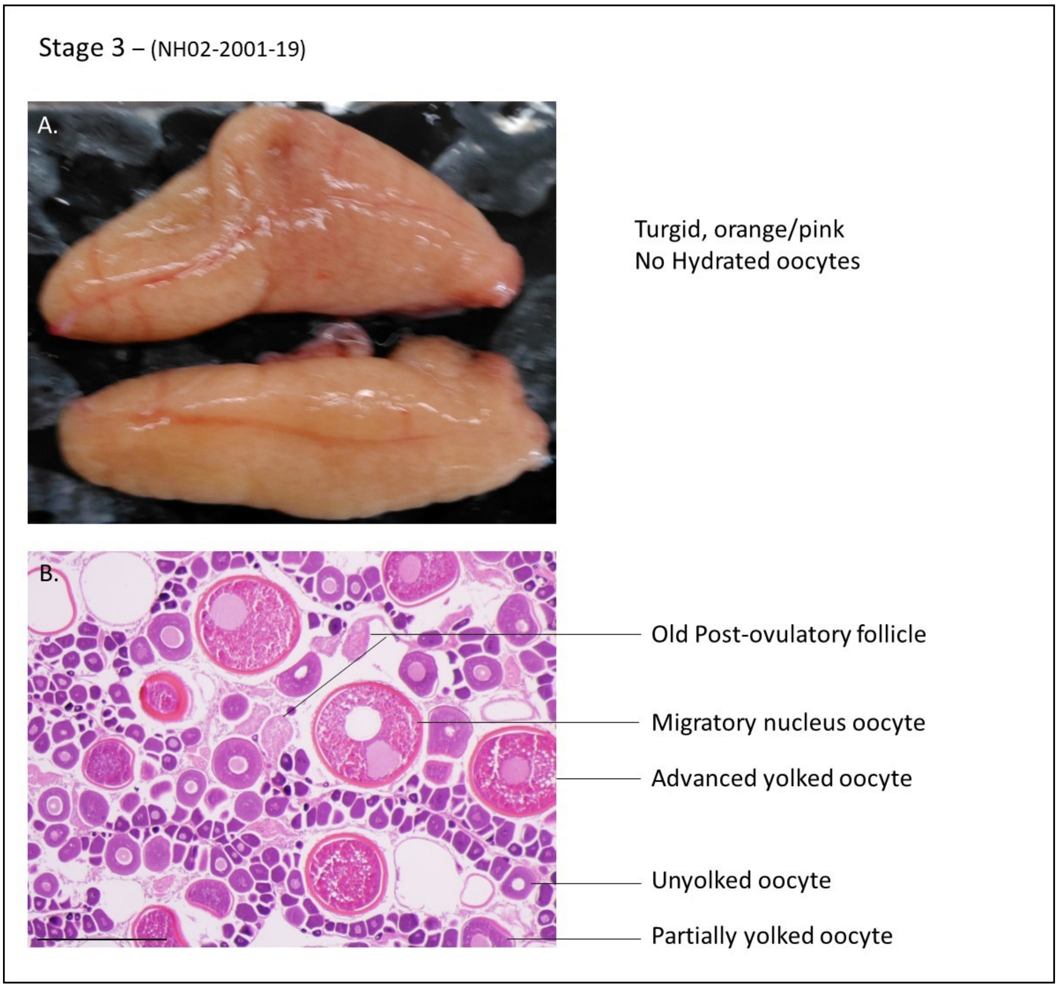


Fig. A2.6. Snapper – NH02/2001-19 (312 mm CFL, 0.74 kg). A. Photograph of whole ovaries. B. Photomicrograph of histological slide from one ovary. Scale bar = 500 µm.

- Presence of degenerating post-ovulatory follicles indicate that spawning had occurred in the past day or so.
- Migratory nucleus oocytes indicate the start of the hydration process, such that spawning would have happened later on the day of capture.

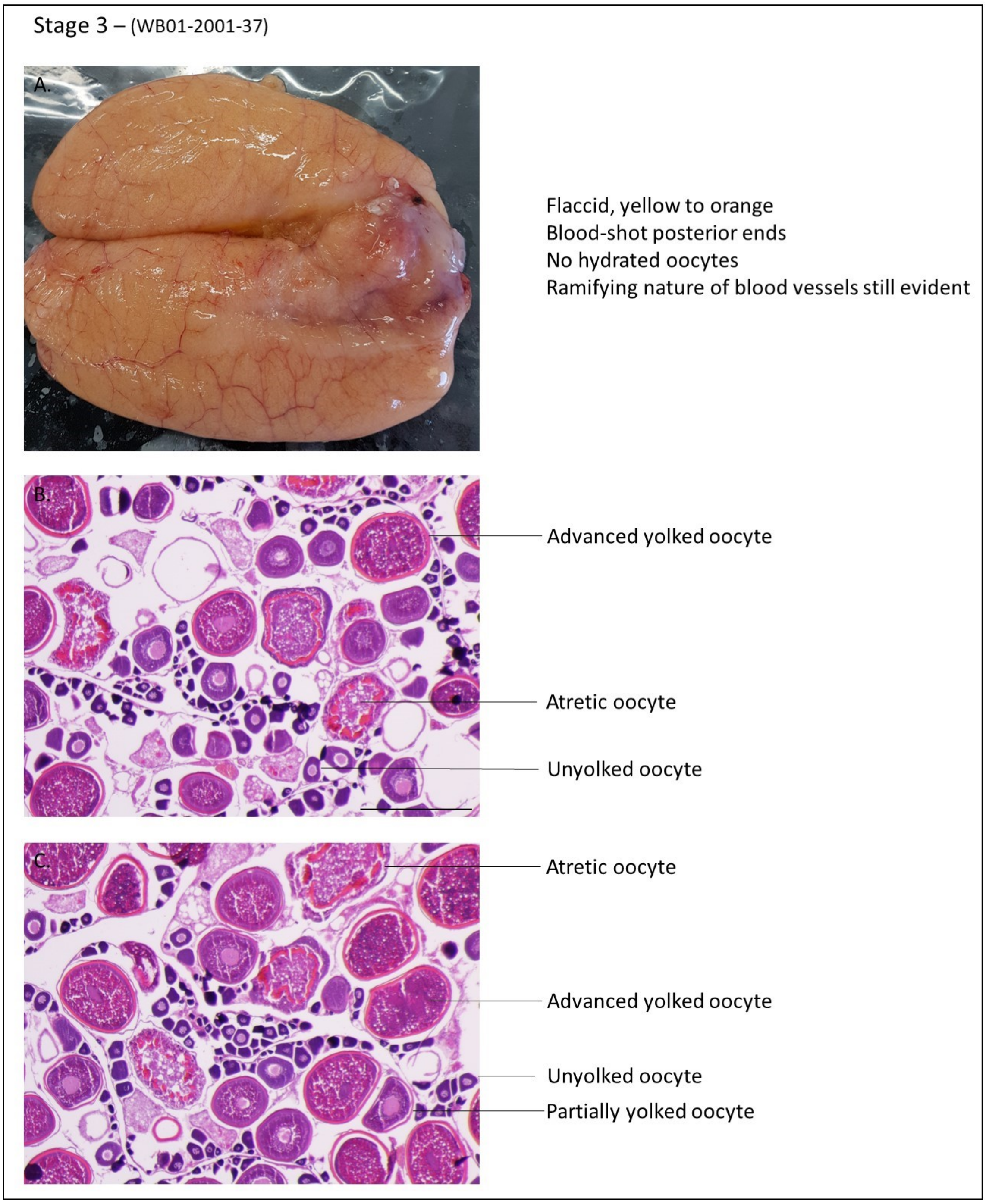


Fig. A2.7. Snapper – WB01/2001-37 (620 mm CFL, 4.43 kg). A. Photograph of whole ovaries. B, C. Photomicrographs of histological slide from one ovary. Scale bar = 500 μm.

- Whole ovaries were quite flaccid, but were still yellow to orange, with individual oocytes apparent.
- Photomicrographs indicate that the most developed oocytes were at the advanced yolked stage.
- A considerable proportion of advanced yolked oocytes were atretic.
- Different stages of atresia are apparent.
- The lack of evidence of recent or impending spawning and high level of atresia suggests that this fish was possibly at or near the end of its spawning season.
- Note that some oocytes show artifacts associated with fixation and histological slide preparation.

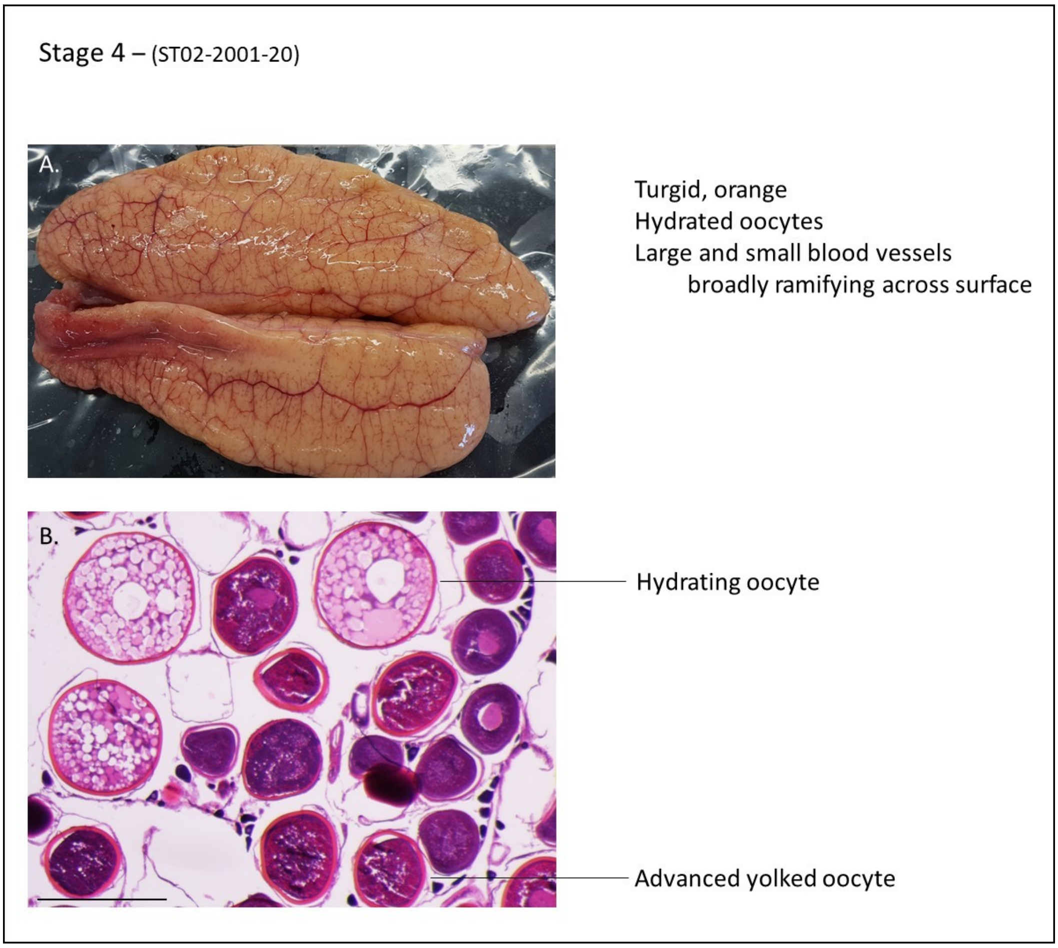


Fig. A2.8. Snapper – ST02/2001-20 (736 mm CFL, 6.51 kg). A. Photograph of whole ovaries. B. Photomicrograph of histological slide from one ovary. Scale bar = 500 µm.

- Whole ovaries were quite turgid and showed hydrated oocytes.
- Photomicrograph showed that the hydration process was relatively early
  - as the hydrated oocytes were still relatively small
  - and yolk platelets were still apparent, i.e., had not coalesced into a homogeneous mass
  - zona radiata were still quite thick.

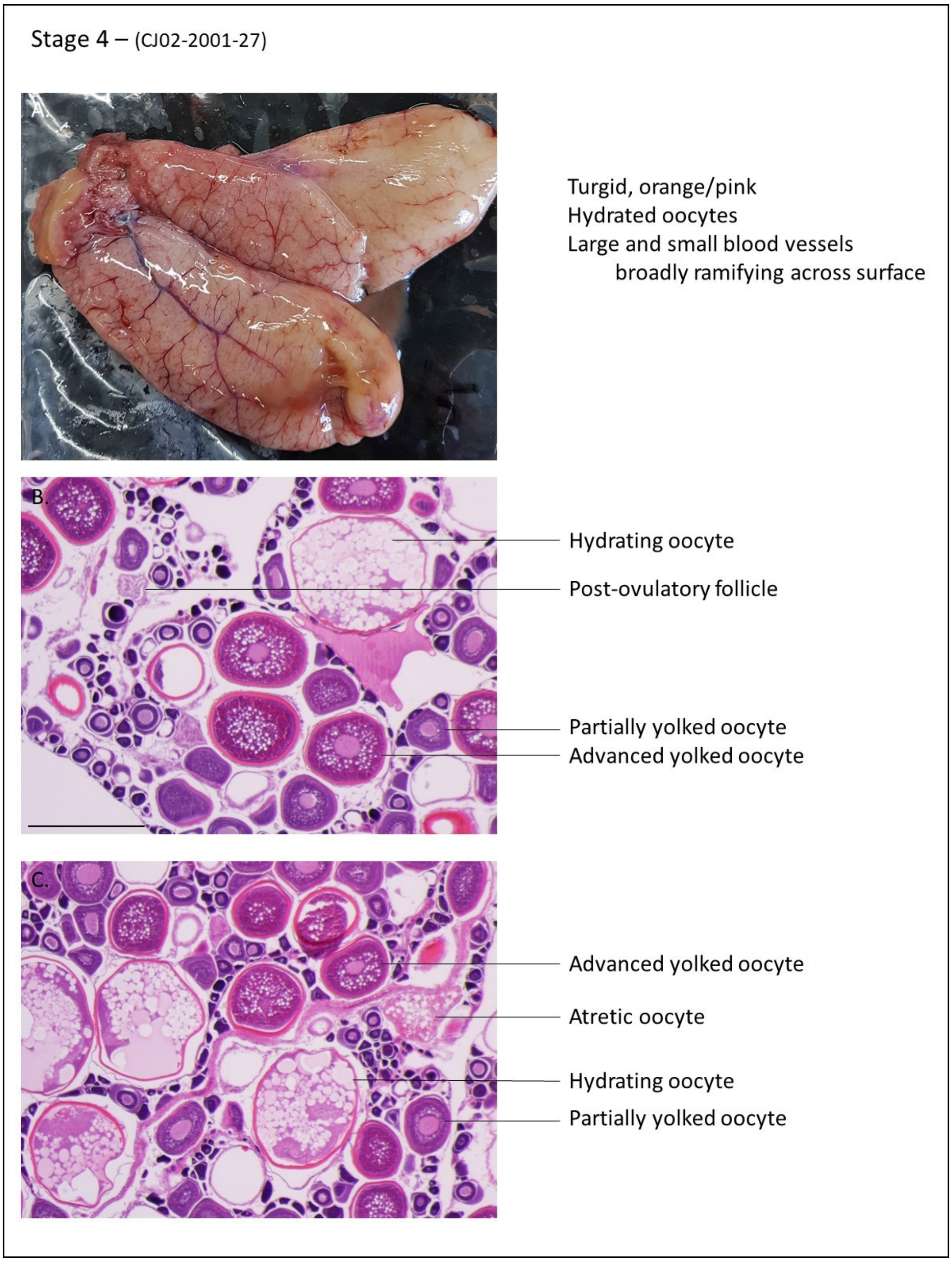


Fig. A2.9. Snapper – CJ02/2001-27 (740 mm CFL, 6.4 kg). A. Photograph of whole ovaries. B, C. Photomicrographs of histological slide from one ovary. Scale bar = 500 μm.

- Whole ovaries were quite turgid and showed hydrated oocytes.
- Photomicrographs showed that the hydration process was relatively early
  - as the hydrated oocytes were still relatively small
  - and yolk platelets were still apparent, i.e., had not coalesced into a homogeneous mass
- Old post-ovulatory follicle indicates that spawning had recently occurred within past day or so.
- There was a minor level of atresia.

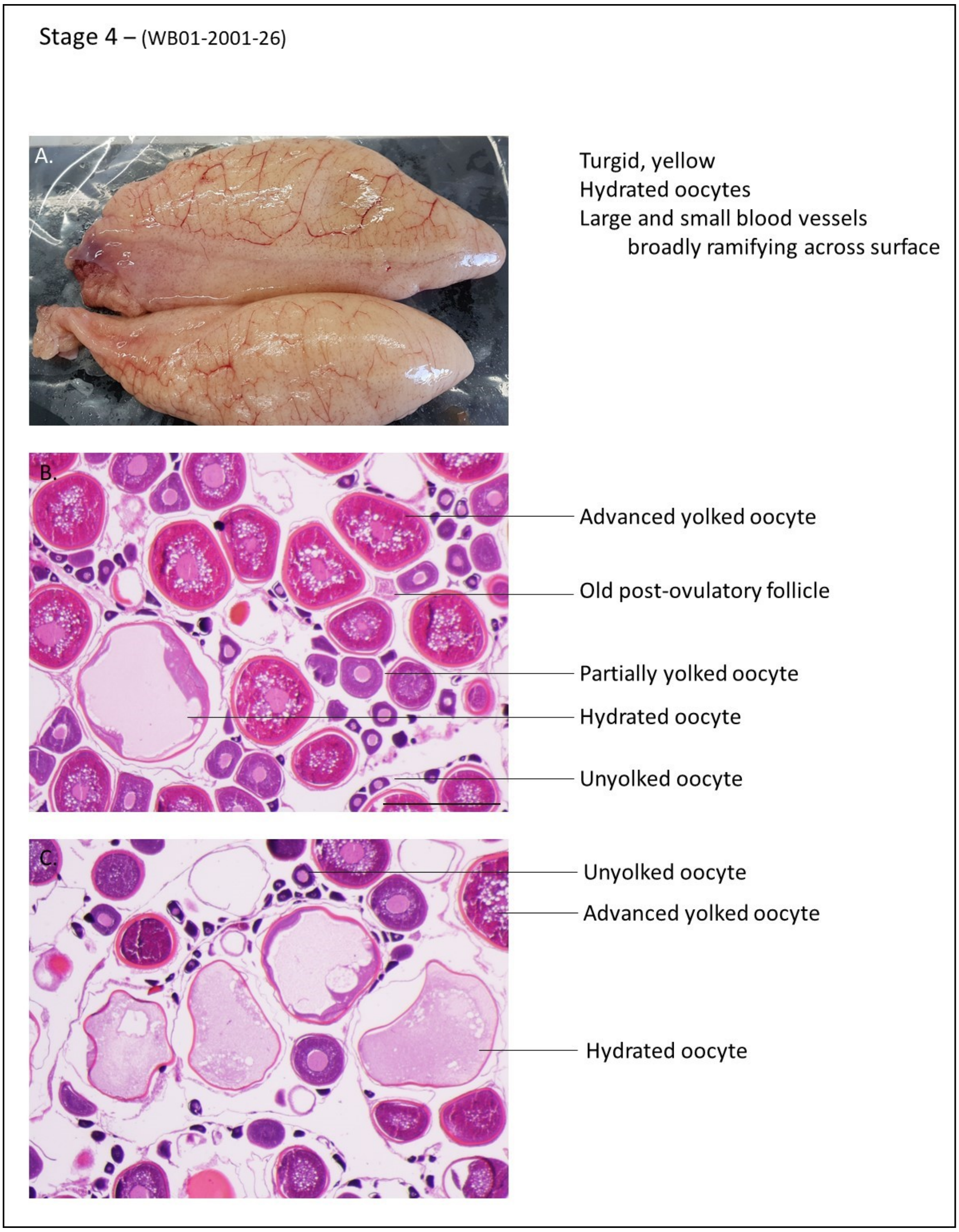
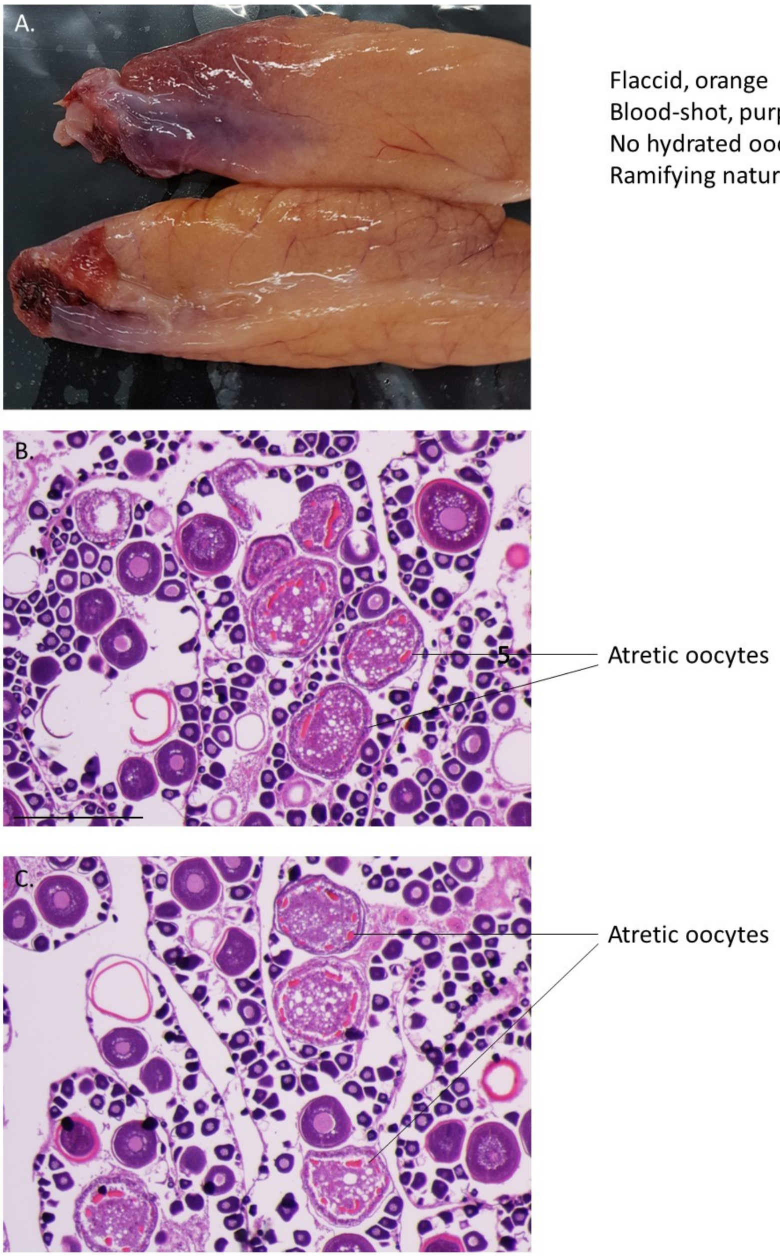


Fig. A2.10. Snapper – WB01/2001-26 (762 mm CFL, 7.3 kg). A. Photograph of whole ovaries. B, C. Photomicrographs of histological slide from one ovary. Scale bar = 500 µm.

- Whole ovaries were quite turgid and showed hydrated oocytes.
- Photomicrographs showed that the hydration process was relatively advanced
  - as the hydrated oocytes were still relatively large
  - and the yolk platelets had coalesced into a homogeneous mass
  - the zona radiata were quite thin.
- Old post-ovulatory follicle indicates that spawning had recently occurred within past day or so.

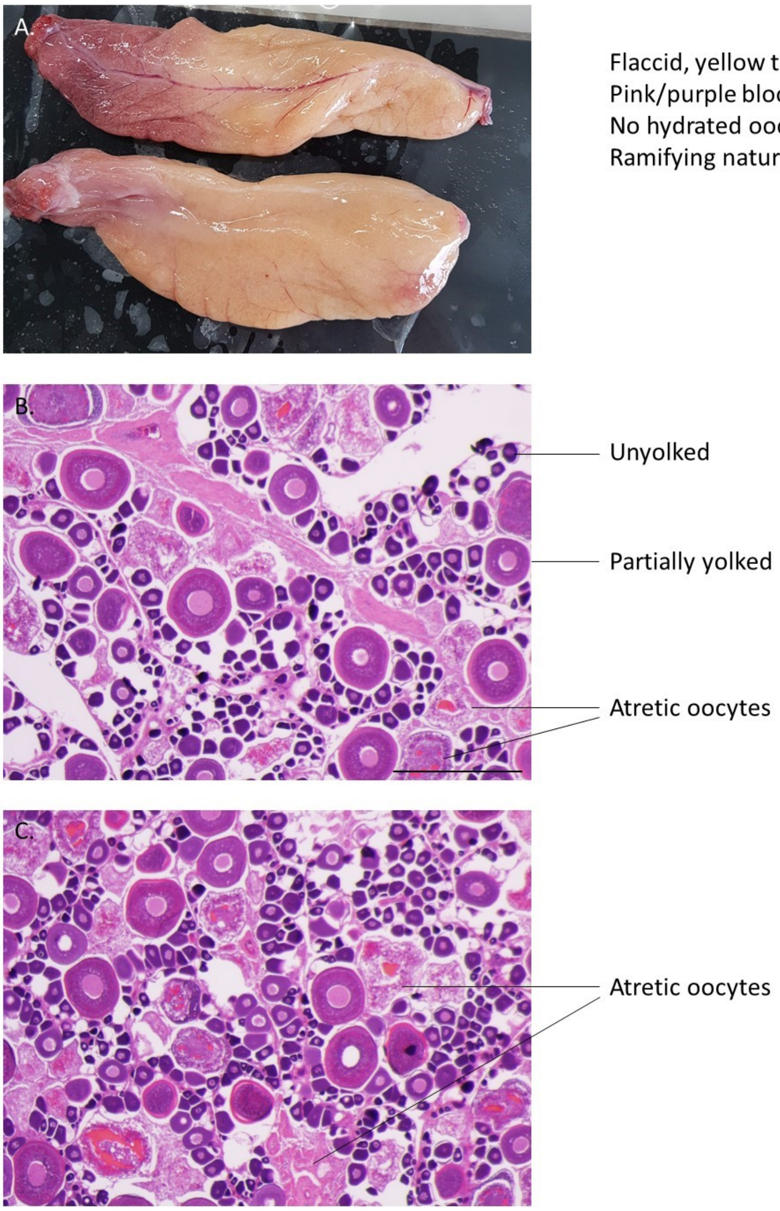
Stage 5 – (BP01/2002-21)



Flaccid, orange
Blood-shot, purple posterior ends
No hydrated oocytes
Ramifying nature of blood vessels decreasing

Fig. A2.11. Snapper – BP01/2002-21 (679 mm CFL, 5.51 kg). A. Photograph of whole ovaries. B, C. Photomicrographs of histological slide from one ovary. Scale bar = 500 µm.

- Whole ovaries were flaccid, orange with no individual oocytes apparent.
- Photomicrographs showed that all large advanced yolked oocytes were atretic
  - the most developed oocytes were only partially yolked
  - there were large numbers of unyolked oocytes.



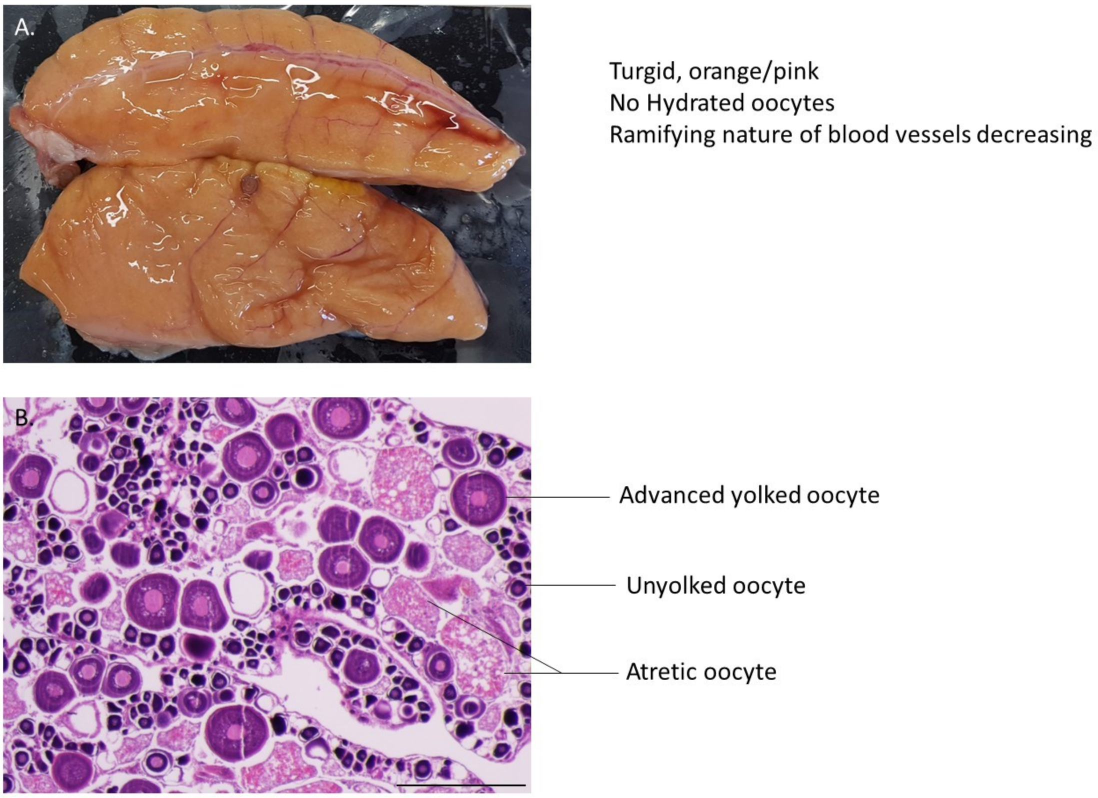
Stage 5 – (BP01/2002-13)

Flaccid, yellow to orange
Pink/purple blood-shot posterior ends
No hydrated oocytes
Ramifying nature of blood vessels decreasing

Fig. A2.12. Snapper – BP01/2002-13 (595 mm CFL, 3.87 kg). A. Photograph of whole ovaries. B, C. Photomicrographs of histological slide from one ovary. Scale bar = 500 µm.

- Whole ovaries were flaccid, no individual oocytes were apparent.
- Photomicrographs showed that atresia was quite advanced
  - the most developed oocytes were only partially yolked
  - all advanced yolked oocytes were atretic.

Stage 5 – (PV02-2004-34)

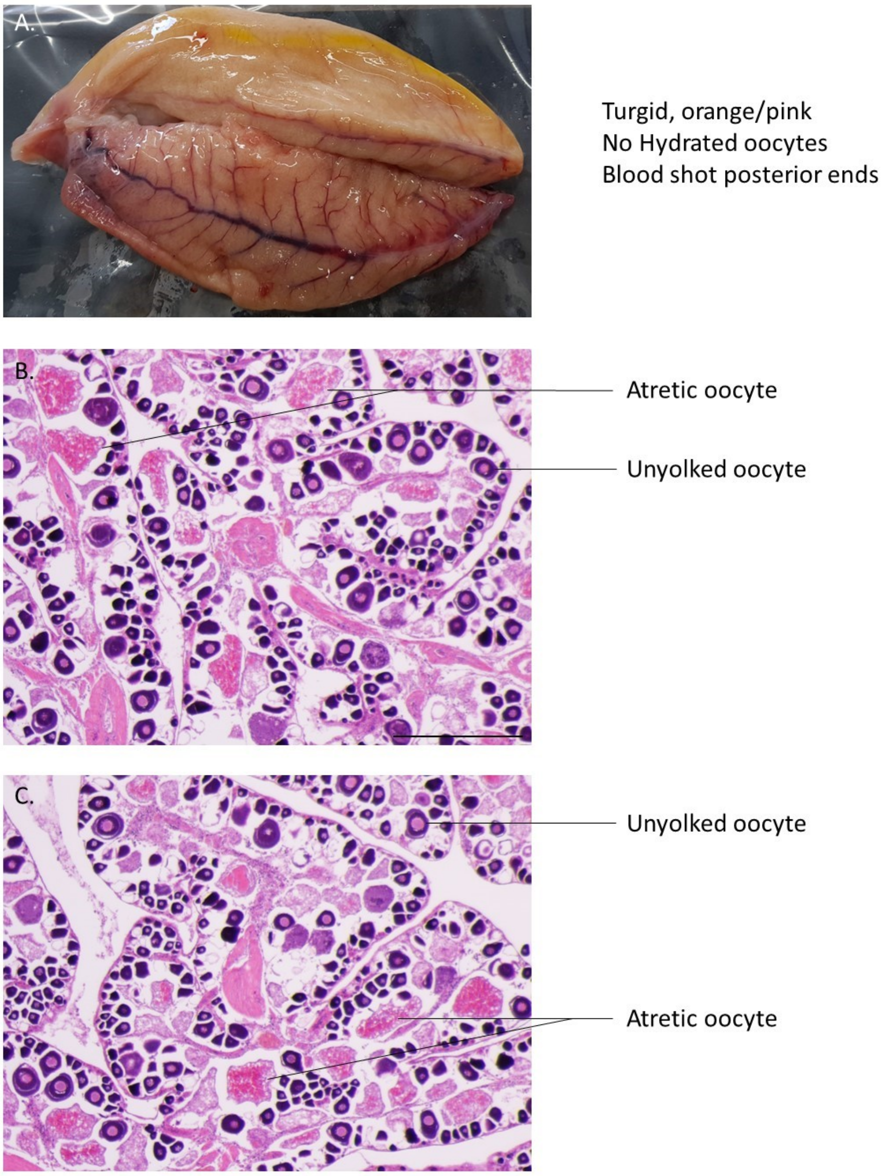


Turgid, orange/pink
No Hydrated oocytes
Ramifying nature of blood vessels decreasing

Fig. A2.13. Snapper – PV02/2004-34 (555 mm CFL, 4.4 kg). A. Photograph of whole ovaries. B, C. Photomicrographs of histological slide from one ovary. Scale bar = 500 µm.

- Whole ovaries were quite turgid, hard and no individual oocytes were apparent.
- Photomicrographs showed that atresia was quite advanced
  - the most developed oocytes were small, advanced yolked oocytes
  - there were no partially yolked oocytes but lots of unyolked ones
  - all large oocytes were atretic.

Stage 5 – (PV02-2006-14)



Turgid, orange/pink
No Hydrated oocytes
Blood shot posterior ends

Fig. A2.14. Snapper – PV02/2006-14 (578 mm CFL, 3.49 kg). A. Photograph of whole ovaries. B, C. Photomicrographs of histological slide from one ovary. Scale bar = 500 µm.

- Whole ovaries were quite turgid and hard and no individual oocytes were apparent.
- Photomicrographs showed that atresia was very advanced
  - no advanced yolked oocytes, few partially yolked ones, dominated by unyolked ones
  - there were numerous atretic oocytes of different sizes and stages.

3. PHENOLOGY OF REPRODUCTIVE BIOLOGY

Anthony Fowler

3.1 Introduction

Most species of fish demonstrate seasonality in their reproductive biology, such that maturation and reproductive activity is restricted to a consistent period of the year (Pankhurst and Porter 2003, Yaran and Sivan 2006, Pankhurst and Munday 2011). This phenology represents a highly evolved system that entails the entrainment of the physiology of the fish to seasonal variation in environmental conditions. Seasonal changes in environmental conditions are detected by the sense organs of the fish, which under appropriate social conditions, stimulate the hypothalamus in the brain. These initiate two pathways of endocrine activity that initiate gonad development and ultimately culminate in the seasonal spawning activity of the fish.

The first role of the hypothalamus-pituitary gonadal axis is to initiate gonad development and meiogenesis (Fig. 3.1a) (Yaran and Sivan 2006, Pankhurst and Munday 2011). The hypothalamus responds to environmental stimuli by producing gonadotropin-releasing hormone (GnRH) into the gonadotropic cells of the pituitary gland. These gonadotropic cells stimulate the production and release of follicle-stimulating hormone (FSH) into the circulatory system. In the gonads, FSH stimulates the secretion of the sex steroids, oestrogen by females and testosterone by males. For both sexes, these hormones stimulate gametogenesis. In the livers of the females, oestrogen stimulates vitellogenesis and production of choriogenins, which are released into the plasma from where they reach the ovaries and are sequestered by the follicles and are incorporated into the oocytes forming the yolk granules and the chorion. So, the consequence of the first endocrine pathway is that the oocytes develop to the advanced yolked stage (Chapter 2).

The second role of the endocrine system of the hypothalamus-pituitary gonadal axis is in the maturation of the developing oocytes (Yaran and Sivan 2006, Pankhurst and Munday 2011). GnRH from the hypothalamus stimulates the release of luteinising hormone (LH) by the pituitary gland (Fig. 3.1b). The post-vitellogenic ovarian follicles respond to the LH by secreting the maturation-inducing hormone, which stimulates the production of the maturation-inducing factor by the oocytes. This stimulates the resumption of meiosis, the final maturation of the oocytes, i.e., the continuation of development from the advanced yolked stage involving the processes of nucleus migration, oocyte hydration and ultimately ovulation and then spawning.

From the description above, it is evident that the seasonality of reproductive activity by adult fish is a complex and sophisticated physiological process that is entrained by the physical environment (Pankhurst and Porter 2003). This seasonal complex of physiological processes that culminates in reproductive behaviour is generally thought to be a mechanism to ensure that the resulting larvae hatch into physical environmental conditions that optimise their chances of survival (Sheaves 2006). However, such seasonality may also reflect constraints on the physiology of the adult biology. There is considerable evidence to indicate that the most significant environmental influences that control the reproductive development of fish are photoperiod and water temperature (Pankhurst and Porter 2003, Pankhurst and Munday 2011). However, since these environmental factors naturally vary concomitantly, their relative influences on the fish are largely confounded, which can make it challenging to dissociate their relative influences. To date, experimental studies have demonstrated that both factors can act as the proximate cue at different stages in the reproductive cycles for different species of fish (summarised in Pankhurst and Porter 2003). As yet, there remains some uncertainty as to how the environmental signals that ultimately culminate in the physiological processes that initiate and maintain reproductive activity are transduced to the fish. For salmonids, the transduction of the photoperiod signal occurs through the inhibitory effects of light on melatonin production by the pineal gland, which is transduced into a reproductive endocrine signal. However, the way in which melatonin modulates GnRH production was not understood (Pankhurst and Porter 2003). The influence of water temperature could be manifested through its influence on reaction-rate increases of endocrine processes or through variations in gene expression and subsequent protein activity in the endocrine cascade. Whilst both photoperiod and water temperature can act as a proximate influence over reproductive development it appears that the situation is further complicated in that their relative influences can vary at different stages through the reproductive cycle and potentially also at different places throughout the range of the species.

The primary focus of this chapter was to develop a more sophisticated understanding of the reproductive biology of Snapper, and the environmental influences to which it is entrained. In South Australia, Snapper reproduction is seasonal (Chapter 2, Saunders et al. 2012). This is also the case for other places throughout the Australasian distribution. However, there is latitudinal variation in the timing of Snapper reproduction (Sheaves 2006, Wakefield 2006). As yet, there is limited understanding of the environmental cues to which the reproductive biology is entrained, and which thereby accounts for such geographic variation in the timing of reproductive behaviour. Nevertheless, developing such an understanding might facilitate more informed fishery management decisions, particularly given the focus since the late 1990s on estimating the spawning biomass using the daily egg production method (McGlennon 2003, Steer et al. 2017, Fowler et al. 2020, Drew et al. 2022), which is heavily dependent on understanding the reproductive biology of the species (Lasker 1985). The empirical approach used here was to provide a synthesis of the spatial information that informs about the seasonality of reproduction of Snapper in South Australia and the associated environmental conditions. Such information was then compared with similar information for other places throughout the Australasian distribution. This was done to document the relationships between reproductive biology and environmental conditions, to describe the adaptive significance of the spatial variation in the timings. To fulfil this aim, the specific objectives addressed were:

1. to provide a comprehensive description of the seasonality of the reproductive biology of Snapper in four different regions in South Australia's gulfs;
2. to synthesise the information on the timing of reproduction of Snapper for several other places throughout the range of Snapper in Australasia;
3. for each region and place considered, to divide the reproductive season into the periods of 'pre-spawning development' and 'spawning', and to identify the peak spawning time. The period of pre-spawning development relates to when the hypothalamus-pituitary gonadal axis has initiated the process of gametogenesis and vitellogenesis, whilst the latter relates to the oocyte maturation processes that culminate in ovulation and spawning (Fig. 3.1);
4. for each region and place, to determine the environmental conditions during the 'pre-spawn development' and the 'spawning' periods of the reproductive season and to consider the relative significance of photoperiod and water temperature in entraining reproductive biology.

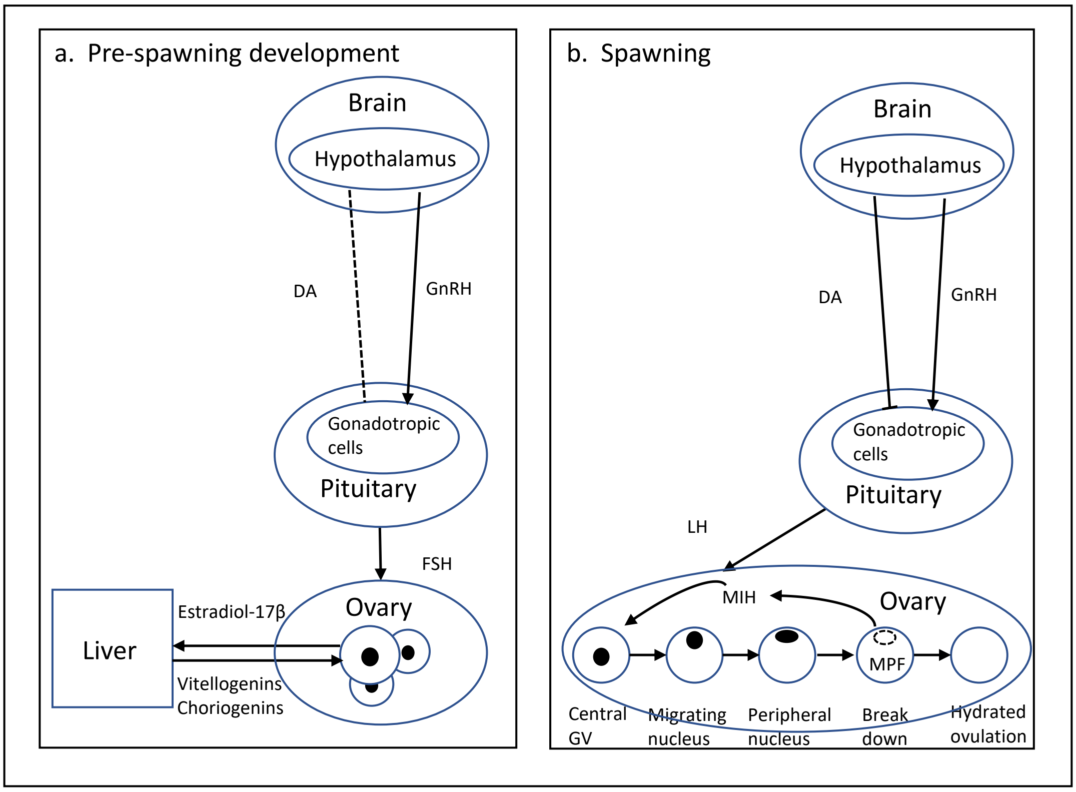


Fig. 3.1. Model showing metabolic pathways that culminate in spawning activity by teleost fishes. a. shows initiation of maturation of oocytes. b. shows continuation of oocyte development that culminates in spawning. DA - dopamine; GnRH – gonadotropin-releasing hormone; FSH – follicle-stimulating hormone; LH – luteinising hormone; MIH – maturation-inducing hormone; MPF – maturation inducing factor.

3.2 Materials and methods

3.2.1 Regional analysis of timing of reproduction

South Australia

The analysis of reproductive biology for Snapper in South Australia is based on data that were collected between 2000 and 2021. Through these years, samples of Snapper were accessed from the commercial and recreational fishing sectors, and during scientific field trips. The samples of fish were generally treated consistently. Where possible, individual fish were measured for caudal fork length (CFL), weighed, and the otoliths were removed to later determine fish age (Chapter 9). The gonads were removed, sexed, and weighed. For each fish, the gonosomatic index (GSI) was calculated as GSI = ((gonad weight) / (fish weight – gonad weight))*100%. The ovaries were classified macroscopically to stage of development considering their size, colour and the visibility of oocytes based on the five stages of development described in Table 3.1. For details regarding microscopic characteristics refer to Chapter 2.

Table 3.1. Stages of development of ovaries from Snapper sampled across South Australia between 2000 and 2021, based on their macroscopic characteristics. For photographs of ovaries at different stages of development and further details regarding associated microscopic characteristics refer to Chapter 2.

Stage	Macroscopic appearance of ovary
1	Ovary small, undeveloped, clear.
2	Ovary small, opaque, light yellow in colour, individual oocytes not discernible.
3	Ovaries relatively large, yellow to orange in colour, individual oocytes discernible.
4	Ovaries large, yellow to orange. Clear, large translucent hydrated oocytes visible amongst smaller opaque ones. Oocytes may be ovulated, located in the oviduct.
5	Ovary small, flaccid, yellow to pink to dark brown.

The estimates of gonosomatic indices and macroscopic staging were considered at the regional scale within the two gulfs, i.e., Northern Spencer Gulf (NSG), Southern Spencer Gulf (SSG), Northern Gulf St. Vincent (NGSV), Southern Gulf St. Vincent (SGSV) (Fig. 3.2, Table 3.2). The numbers of females sampled varied amongst regions, and for individual regions varied amongst years (Appendix 3.6.1). Because of the north-south orientation of the gulfs these four regions extended across three degrees of latitude. For each region, the data from 2000 to 2021 were combined across years to provide monthly estimates of gonosomatic indices and the frequencies of females at the different macroscopic stages of ovary development. Then, to provide a finer-scale temporal analysis of the macroscopic stage data, they were considered at the daily temporal scale. The total numbers of fish sampled and classified to the five different stages of development on each day through the period of 1st October to 31st March were accumulated across years and were plotted against day-of-the-year.

Other Australasian places

Information on the timing of reproduction by Snapper from different places throughout Australasia were compiled and compared. Such information was accessed from journal articles, reports and theses and through direct communication with fishery scientists. Apart from that, for South Australia the data came from sampling programs that were done at different times between the mid-1980s up to 2008 (Table 3.2). For regions in Queensland, New South Wales, Victoria, Western Australia, and New Zealand the reproductive seasons were identified based on published estimates of gonosomatic indices and estimates of relative numbers of gonads at the different macroscopic stages (Chapter 2). For Cockburn Sound in Western Australia, the reproductive characteristics were based on ichthyoplankton sampling events done between 2001 and 2004, with the spawning season identified by the presence of Snapper eggs in the plankton samples (Wakefield 2010).

For all regions, the duration of the reproductive season was identified based on gonosomatic indices and the frequencies of the macroscopic stages of ovaries. The seasons were divided into the periods of ‘pre-spawning development’ and ‘spawning’. Because information was not available on the microscopic characteristics of ovaries from histological analyses for individual fish, this division was based on the reported macroscopic stages of the females. Fish at macroscopic stages 2 and 3 (i.e., up to the advanced yolked stage) were classified to the ‘pre-spawning’ development period (Fig. 3.1a), whereas the ‘spawning’ period was determined by the presence of fish with ovaries classified to Stage 4 (Fig. 3.1b). This division reflects the hiatus in development of the oocytes relating to the two endocrine pathways. For the latter, the presence of hydrated oocytes is a sure sign of the influence of the second pathway (Fig. 3.1b), and that the fish was preparing to spawn on the day of its capture (Chapter 2).

3.2.2 Regional environmental characteristics

For the South Australian regions and elsewhere around Australia, the average monthly water temperatures were determined for the identified reproductive season. Estimates of water temperature were accessed either from the published study or as estimates of sea surface temperature (SST) from satellite imagery provided by CSIRO. The latter data on SST were requested for rectangular blocks that encompassed large areas of marine waters that incorporated the specific areas from which the fish had been sampled and for the period of sampling. For South Australia, average daily estimates of SST were provided for the years of 1994 to 2012.

Estimates of photoperiod were based on the times of sunrise and sunset at the nearest major centre to the various regions considered. They were accessed for the year 2013 from the website http://www.timeanddate.com/worldclock/sunrise.html and assumed to apply for the earlier years.

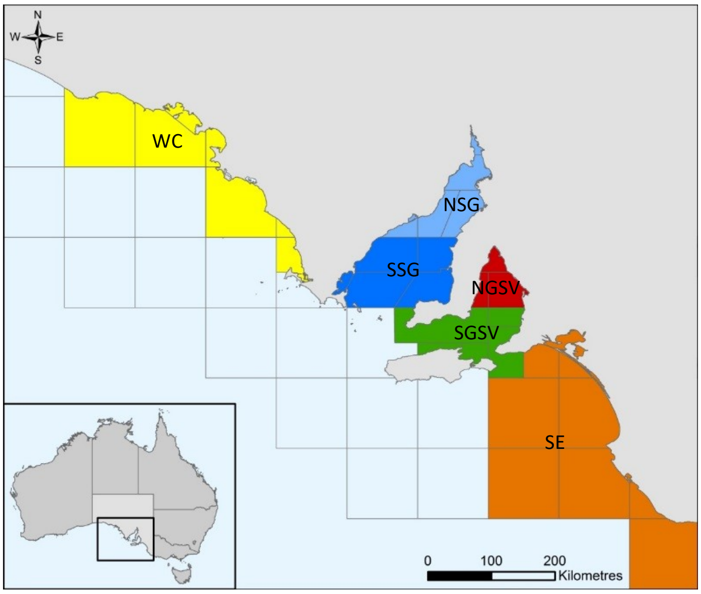


Fig. 3.2. Map of South Australia showing the regions that are considered in stock assessments and studies on population biology. The regions considered in this analysis of reproductive biology were: Northern Spencer Gulf (NSG), Southern Spencer Gulf (SSG), Northern Gulf St. Vincent (NGSV), Southern Gulf St. Vincent (SGSV).

Table 3.2. Summary table showing the details for places for which reproductive information for Snapper were considered. For each geographic region, the data show the regions considered, the latitudinal range, and the dates through which reproductive data were collected.

Geographic region	Region	Latitude	Dates	Reference
South Australian gulfs	Northern Spencer Gulf	33 – 34°S	2000-21	Saunders et al. (2012), unpublished data
	Southern Spencer Gulf	34 – 35°S	2000-21	unpublished data
	Northern Gulf St. Vincent	34 – 35°S	2000-21	unpublished data
	Southern Gulf St. Vincent	35° 20’ – 36°S	2000-21	unpublished data
Central Queensland		21 – 24°S	1994/95	Ferrell and Sumpton (1998)
SE Queensland	Fraser	24° 30’ – 26°S	1992-95	Sumpton (pers. Comm.)
	Moreton	26° 30’ – 27° 30’S	1992-95	Sumpton (pers. Comm.)
New South Wales	North	30° 17’S	1986/87	Ferrell (pers. Comm.)
	Central (a)	33° 30’S	2003-08	Stewart (pers. Comm.)
	Central (b)	34° 30’S	2003-08	Stewart (pers. Comm.)
Victoria	Port Phillip Bay	38°S	1997-98	Coutin et al. (2003)
Western Australia	Cockburn Sound	32°S	2001-04	Wakefield (2006, 2010)
	Shark Bay–Denham Sound	26°S	1997-04	Jackson et al. (2010)
	Shark Bay–Freycinet Estuary	26°S	1997-2004	Jackson et al. (2010)
New Zealand	Hauraki Gulf	36° 30’	1988-91	Scott and Pankhurst (1992)

3.3 Results

3.3.1 Timing of reproduction and associated environmental conditions

South Australia – regional SST regimes

The four different gulf regions of South Australia have different water temperature regimes. For NSG, the extremes in average monthly SSTs were between July and February for which the average temperatures increased from 13.1 to 24.4 °C, respectively (Fig. 3.3). For NGSV, the seasonal range was 12.8 to 23.2 °C. For the southern gulfs, the ranges were less extreme, with the coldest month in August and the warmest in February. For SSG, the seasonal extremes were from 13.7 to 22.9°C, and for SGSV the range was from 13.7 to 20.4°C. These observations are consistent with those from previous studies which show that the heat budgets for the gulfs are dominated by surface heat exchange that results in seasonal water temperature gradients up the gulfs (Nunes and Lennon 1986, de Silva Samarasinghe and Lennon 1987).

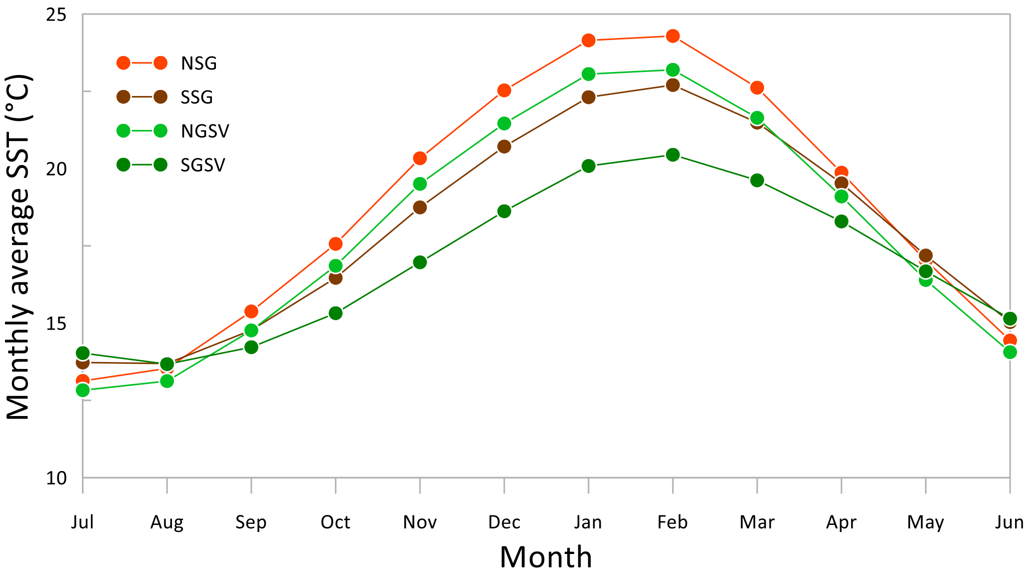


Fig. 3.3. Average monthly estimates of SST for the South Australian gulf regions for the years of 1994 to 2012, based on satellite imagery.

Northern Spencer Gulf

For NSG, the seasonality in reproduction was evident based on 2,763 females sampled between 2000 and 2021 (Appendix Table A3.1). The sample sizes varied considerably amongst years, particularly declining over the past decade as the status of the fishery declined. The average monthly gonosomatic indices for females were low between March and September, increased marginally in October, then substantially in November, remained high in December before declining in each of January, February and then back to the base level in March (Appendix Fig. A3.1a). These changes relate to Stage 3 fish first becoming apparent in October, whilst spawning fish were first detected in November, increased in December and then declined in January and February, whilst those at Stage 5 increased from December onwards (Fig. A3.1b).

The assessment of macroscopic staging by day-of-the-year throughout the spawning season provided greater resolution regarding the timing of stages throughout the reproductive season. In October, Stage 3 fish were evident throughout the month but were few relative to the earlier stages (Fig. A3.1c). Whilst the first spawning fish were detected in early November, it wasn't until the 20th November when a high proportion of fish were spawning. Through December until mid-January relatively high proportions of sampled fish were spawning. From mid-January, the incidence of spawning fish was low, whilst the proportion of those at Stage 5 increased considerably. In February, most fish were classified to Stage 5 and then to Stage 2. There were also a few instances of fish classified to Stage 4, but there was some doubt about these (Fig. A3.1c). Several samples involved small, old fish that are typical of fish from SSG (Fowler et al. 2004), having been associated with the port-of-landing of Wallaroo. It is highly likely that these fish were taken in SSG and then incorrectly assigned to NSG. The other samples assigned to NSG that were classified to Stage 4 were captured from the wreck of the Estelle Star. This is located on the boundary between NSG and SSG and should not be considered typical for NSG.

The analysis of reproductive information from samples collected in NSG indicate that the duration of the spawning season primarily extended from November to January, with the peak period between mid-November and mid-January (Fig. A3.1c).

Southern Spencer Gulf

For SSG, there were 1,471 females sampled between 2000 and 2021, with the numbers highly variable amongst years (Appendix Table A3.1). The pattern of variation in average monthly estimates of GSI differed from NSG, as they increased more slowly in October to December, but then declined more slowly between December and April (Fig. A3.2a). A few fish with Stage 3 ovaries were collected in September and October and then increased in November (Fig. A3.2b). The first spawning fish were sampled in December and were detected until March.

For SSG, few fish were sampled in the month of November across all years. From the 3rd December onwards, a high proportion of females were spawning (Fig. A3.2c). On the 7th December, a sample from MFA-33 from the port-of-landing of Port Victoria involved a high proportion of spawning fish. Through January, February and March, spawning fish continued to be sampled from SSG. Up to 22nd and 23rd March 2021, samples of Snapper with spawning fish were collected from MFAs 30 and 33 in the southern part of the gulf.

The spawning season for this southern region extends from at least early December until late March. The low sample sizes in November compromised determining when spawning commenced.

Northern Gulf St. Vincent

For NGSV there were 1,864 females sampled, predominantly from 2008 onwards (Appendix Table A3.1). The average gonosomatic indices were low from March to September, increased from October to the maximum in December before declining considerably in January and February (Appendix Fig. A3.3a). Stage 3 ovaries were evident in October and November. The first spawning fish were detected in October, relating to two fish sampled from Port Clinton. Few fish were sampled throughout November. From early December, the samples were dominated by fish at Stages 3 and 4 (Fig. A3.3b,c). Evidence for spawning activity continued through January and into February. The proportions of fish at Stage 5 increased through latter January and was high from early February onwards. In February, spawning fish were sampled in the southern part of the region, i.e., near Port Vincent and Stansbury. The latest spawning fish were collected on the 12th February 2014 in MFA 36 out of North Haven. After this, a few Stage 3 fish were sampled, but most were at Stages 2 and 5. These results indicate that the timing of the spawning season for this region is from mid-October to mid-February.

Southern Gulf St. Vincent

For SGSV there were 1,069 females considered for their reproductive status (Appendix Table A3.1). The gonosomatic indices were low from April to September, increased from October to December, before declining until April (Fig. A3.4a). The fish sampled in July, August and September were classified to Stages 2 and 5 (Fig. A3.4b). Several fish that were captured in MFAs 40 and 44 in October were classified to Stage 3 (Fig. A3.4c). Several spawning fish were captured in November, with the earliest on the 8th, and the other two later in the month. On the 1st December several spawning fish were sampled from MFAs 40 and 44. Most fish captured throughout December, January and February were at Stages 3 and 4. The relatively high numbers taken on the 15th and 19th February were taken in MFA 44. The numbers of fish at Stage 5 increased towards the end of February. In early March, two spawning fish were captured in MFA 40, although most sampled throughout March were classified to Stages 2 and 5. These data suggest that the duration of the spawning season in SGSV is from November until early March.

South Australia – pre-spawning and spawning conditions

In the four South Australian regions, gonad development was evident as early as September, but definitely by October. The average monthly SSTs for October ranged from 15.3°C for SGSV to 17.6°C for NSG. Estimates of daylength increased during the pre-spawning period from 12.25 to 13.5 hours. By December, the highest proportions of females were spawning when the regional estimates of average water temperature ranged from 18.6 to 22.5°C. Consequently, the timing of spawning in South Australia corresponded with the higher water temperatures of late spring – summer. There were considerable differences in the duration of the spawning seasons between the northern and southern gulfs. NSG had the most contracted spawning season, with spawning declining in January and essentially finishing by February when the mean monthly SSTs exceeded 24°C. Alternatively, for each of SSG and SGSV, which had considerably lower temperatures, spawning continued through until late February or March. For NGSV, which had a spawning season of duration longer than that for NSG but less than for the southern regions, the SST regime was intermediate between these.

Queensland

Data on the reproductive biology of Snapper are available from several studies done in the waters of central Queensland (Ferrell and Sumpton 1998), as well as at two regions in south-east Queensland (Sumpton pers. comm). Despite the sizes of these regions and the distances between them, the timing of the reproductive seasons were similar, encompassing autumn to early spring (Table 3.3). Pre-spawning gonad development occurred in April and May, which led to spawning through the months of June to October with peak spawning in the winter months of July and August.

The pre-spawning development for the Queensland regions occurred through the months of autumn, i.e., April and May during which time water temperature declined from 25.2°C to 24.2°C (Table 3.3). Furthermore, photoperiod declined from 11.75 to 10.5 hours (Table 3.3). Then, spawning occurred through the winter months of June to September when the water temperature range was 21.7 – 23.2°C. During the peak spawning period of July and August, the temperature range was limited to 21.7 to 22.3°C. Estimates of GSI declined in September, which indicates that reproductive activity was waning. They continued to decline as water temperature increased during spring. Overall, reproductive activity was inversely related to water temperature and photoperiod.

New South Wales

Limited data were available from studies on reproductive development of Snapper in the regional waters of both northern and central NSW. For the former, during the 1980s, GSI's for both sexes were low from December to May before they increased in June and July. They attained their maxima in August and then declined through September to November. From this, it is assumed that pre-spawning development occurred through June, which led to the start of spawning in July that peaked in August and then declined to November (Table 3.3). In June, the SST had fallen to 20.4°C and photoperiod to about 10 hours. The SST during peak spawning was 19.4°C.

The reproductive data for Central NSW are less reliable as they were based on few fish sampled across several years, and sampling was not done in every month of the year. For fish from the waters of latitude 33° 30'S, the data indicated peak spawning during August, with subsequent activity declining to November (Table 3.2). This suggested that peak spawning corresponded to the time of minimum water temperature of 17.5°C. In contrast, the GSI's from fish captured at latitude 34° 30'S remained relatively high during November and December, suggesting a relatively later reproductive season, with peak spawning corresponding to the SST of 19.5°C.

Victoria

Port Phillip Bay (PPB) is the main spawning ground and nursery area for the Western Victorian Stock of Snapper (Hamer et al. 2011). Sampling of adults to determine the reproductive season was done between October 1997 and October 1998, through which the monthly average water temperatures ranged from 11.0 to 20.5°C (Table 3.3). Gonad development occurred during the spring months of September and October, when water temperatures increased from 12.5 to 14.5°C and daylength increased from 11.25 to 13.5 hours. Then, spawning started in November and continued through until February, corresponding to summer monthly averages of 16.5 to 20.5°C. The peak spawning month was December when the average monthly water temperature was 18.5°C. Nevertheless, the hatch dates, as determined from otolith analyses for 0+ Snapper captured in Port Phillip Bay were from late October to late February, with the peak through November and numbers declining through December, January, and February (Hamer pers. comm.).

Western Australia

There are two significant spawning locations for Snapper on the west coast of Western Australia that are separated by approximately 6° of latitude, i.e., Shark Bay in the central part of the west coast and Cockburn Sound near Perth in the southwest. At the latter location during the years of 2001 to 2004, the timing of the reproductive season was during spring-summer, i.e., between September and January, relating to a water temperature range of 17-24°C (Table 3.3). Here, the pre-spawning development period was nominated as September when few eggs were captured (Wakefield 2010). The average temperature was 16.9°C, whilst the photoperiod increased from 11.5 to 12.5 hours. During the peak spawning month of November, the average water temperature was 20.4°C.

The timing of reproduction for Snapper in two areas in Shark Bay contrast with that from Cockburn Sound in that pre-spawning development corresponded with declining water temperatures and photoperiods during autumn, and peak spawning times corresponded approximately with low winter water temperatures and short day-lengths (Table 3.3). In Denham Sound, pre-spawning development occurred in March during which the average water temperature was 25.2°C and daylength declined from 12.6 to 11.8 hours. During the spawning period of April to September, the average water temperature declined from 25.3 to 20.1°C before increasing again. Peak spawning occurred during July when the average temperature was 20.8°C. Despite the proximity of the Freycinet Estuary to Denham Sound, the timing of reproductive activity differed by a month or two. For this area, pre-spawning development extended until May, and spawning occurred from June to October with the peak in August. The spatial differences reflected lower water temperatures in Freycinet Estuary.

Table 3.3. Summary of results comparing the timing of reproduction of Snapper and the environmental conditions at various places throughout the Australasian distribution.

Region	Temperature range (°C)	Photoperiod range (hours)	Pre-spawning Period	Spawning period	Peak spawning period	Photoperiod in pre-spawning (hours)	SST during pre-spawning (°C)	Range in SST during spawning (°C)	SST during peak spawning (°C)	Duration of spawning (months)
SA-NSG	13.1 – 24.4	9.75 – 14.5	Oct	Nov to Jan	Dec	12.5 – 13.5	17.6	20.3 – 24.1	22.5	3
SA-SSG	13.7 – 22.9	9.75 – 14.5	Oct	Nov to Mar	Dec	12.5 – 13.5	16.5 – 19.0	18.7 – 22.7	20.7	5
SA-NGSV	12.8 – 23.2	9.75 – 14.5	Oct	Mid-Oct to mid Feb	Dec	12.5 – 13.5	16.8	19.5 – 23.2	21.5	4
SA-SGSV	13.7 – 20.4	9.75 – 14.5	Oct	Nov to Mar	Dec	12.5 – 13.5	15.3	17.0 – 20.4	18.6	5
Central Qld			Apr to May	Jun to Sep	Jul to Aug					4
SE Qld	21.7 - 26.3	10.5 - 14	Apr to May	Jun to Oct	Jul to Aug	11.75 – 10.5	25.2 – 24.2	21.7 – 23.2	21.7 – 22.3	5
North NSW	19.4 – 24.7	10.2 – 14.1	Jun	Jul to Nov	Aug	10.2 – 10.3	20.4	19.4 – 21.9	19.4	5
Central NSW (a)	17.5 – 22.8	10 – 14.5	pre-Aug	Aug to Oct	Aug	10 – 10.5	<17.5	17.5 – 18.4	17.5	3
Central NSW (b)	17.1 – 22.5	10 – 14.5	pre-Oct	Oct to Dec	Nov	11.5 – 12.5	<18.5	18.5 – 20.7	19.5	3
Vic -PPB	11.0 – 20.5	9.5 – 14.45	Sep to Oct	Nov to Feb	Dec	11.25 -13.5	12.5 – 14.5	16.5 – 20.5	18.5	4
WA-CS	15.7 – 23.6	10 – 14.25	Sep	Sep to Jan	Nov	11.5 – 12.5	16.9	16.9 – 23.6	20.4	5
WA-DS	19.4 – 26.5	10.25 - 14	Mar	Apr to Sep	July	12.6 - 11.75	25.2	20.1 – 25.3	20.8	6
WA-FE	16.4 – 26.9	10.25 - 14	Mar to May	Jun to Oct	Aug	12.6 – 10.5	26.5 – 21.4	16.4 - 19.1	16.4	5
NZ-HG	14.2 – 20.8	9.6 – 14.6	Sep	Oct to Feb	Nov	11.25 - 12.5	<15	15.6 – 19.9	17.0	5

New Zealand

During the late 1980s-early 1990s, in the Hauraki Gulf, pre-spawning development occurred during September when water temperature remained below 15°C, and photoperiod increased from 11.3 to 12.5 hours (Table 3.3). Then spawning occurred between October and February during which the average temperature range was from 15.6 to 19.9°C. The peak spawning month was November when the average water temperature was 17°C. Successful recruitment, based on analysis of otoliths from juvenile fish, varied amongst years but was generally concentrated in November and December but ranged from as early as September and extended until early March (Francis 1994).

3.3.2 Synthesis of information across regions

This synthesis considers the environmental conditions under which reproductive development and spawning occurred at the latitudes of the different regions. First, there was a highly significant linear relationship between average annual SST and latitude, which accounted for 87% of the variation in average SST (Fig. 3.4a) (Table 3.4). The more southern, temperate locations had lower annual average water temperatures than did the semi-tropical, low latitude localities. For each region, the difference in timing between the month of peak spawning and the month with the lowest average water temperature was calculated. These estimated deviations were plotted against latitude, and gave a significant positive linear relationship, whereby latitude accounted for 43% of the variation in the estimated deviations (Fig. 3.4b) (Table 3.4). As latitude increased, the difference in timing between peak spawning and the month of minimum SST also increased. Populations at low latitudes spawned during relatively cool months, whereas those in high latitudes spawned during warmer months. In contrast, there was no relationship between the monthly average water temperature at the peak spawning time and latitude. Rather, the SSTs during the ‘peak’ spawning months were restricted to the temperature range of 17-22°C but did not vary systematically with latitude (Fig. 3.4c).

For consideration of photoperiod regimes, the deviations in timing between the month of peak spawning and the month of minimum daylength were calculated and plotted against latitude. There was a highly significant linear relationship between the temporal deviations and latitude that accounted for 68% of the variation in the temporal differences (Fig. 3.4d) (Table 3.4). This means that for the populations located in the lower latitudes, the peak spawning time was relatively close to the time of year of minimum daylength, whereas for fish in the higher latitudes peak spawning corresponded more closely with the timing of maximum daylength.

Table 3.4. Summary table showing the relationships between SST and latitude and with the peak spawning times for the places throughout Australasia for which data on reproductive biology of Snapper were accessed.

Variable	Relationship	n	r^2
SST_{ave} - average annual SST	SST_{ave} = -0.5315(latitude) +36.84	13	0.8688
Dev_t - Deviation between month of peak spawning and month with lowest SST	Dev_t = 0.3272(latitude) – 7.7822	13	0.43
SST_p – monthly SST at peak spawning		13	-0.059
Dev_p – Deviation between month of peak spawning and month with minimum daylength	Dev_p = 0.3983(latitude) – 8.7756	13	0.6766

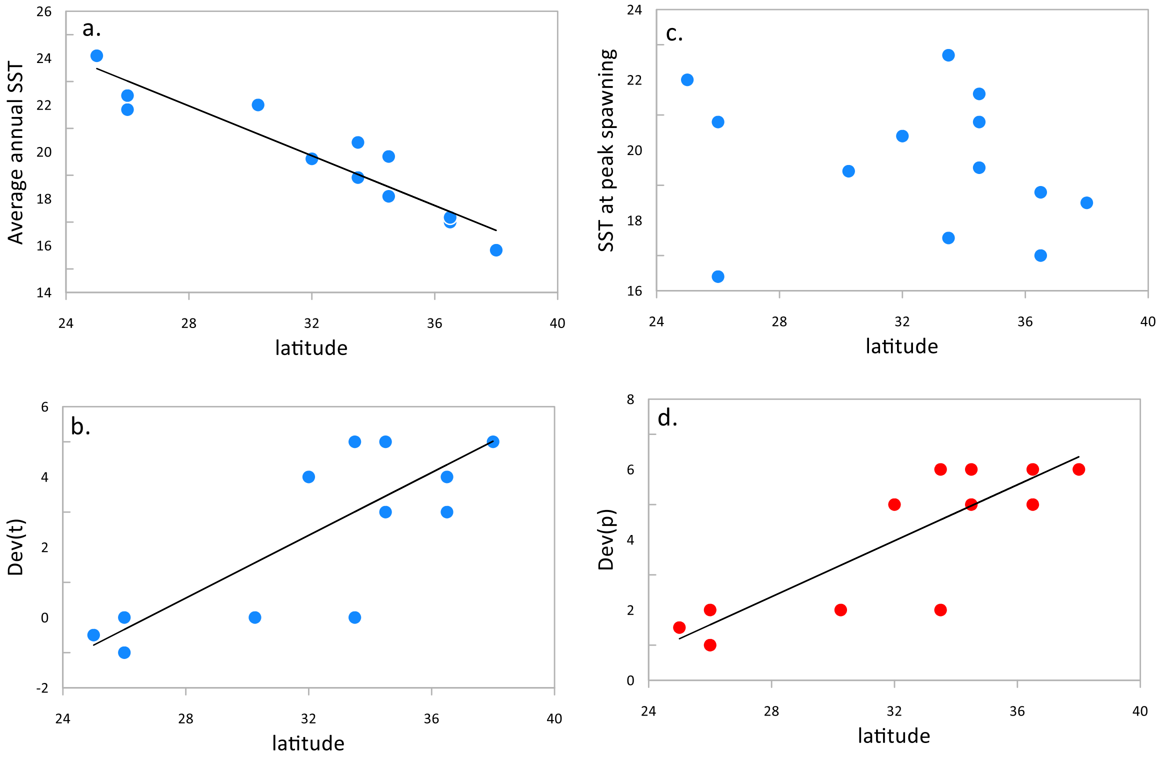


Fig. 3.4. Summary of results comparing environmental characteristics for when Snapper spawn with latitude. a. Relationship between average annual SST and latitude, for regions in Table 3.1. b. Relationship between deviation in months between peak spawning month and month of minimum SST against latitude. c. Comparison of mean monthly SST during the peak spawning month with latitude (Table 3.4). d. Relationship between deviation in months between peak spawning month and month of minimum photoperiod.

3.4 Discussion

As the populations of Snapper in southern Australia and New Zealand are fundamentally driven by inter-annual variability in recruitment of the 0+ year class, there has been and continues to be a focus on trying to understand this variability (Francis 1994, Fowler and Jennings 2003, Hamer and Jenkins 2004). To achieve this, it would be highly beneficial to have a comprehensive understanding of the reproductive biology of Snapper and the extent to which it is influenced by environmental factors. This chapter focussed on describing the phenology in reproduction of Snapper at two spatial scales, i.e., amongst the regions of the South Australian gulfs, and amongst numerous distant places that support important Snapper fisheries located throughout the sub-tropical and temperate zones of Australasia. The purpose was to consider the timing and duration of the reproductive seasons and to assess the influence of different environmental factors on them.

3.4.1 Seasonality of Snapper reproduction in South Australia

The study of Snapper reproduction in South Australia largely focussed on the geographic region that included the two semi-enclosed seas of Spencer Gulf and Gulf St. Vincent as well as Investigator Strait that is bounded on its southern edge by the north coast of Kangaroo Island. Historically, Snapper populations and their fisheries have been concentrated in this geographic region (Chapter 1, Fowler et al. 2020). For stock assessments and studies on population biology this geographic region is generally divided into four essentially contiguous regions i.e., NSG, SSG, NGSV and SGSV. This part of the southern Australian coastline is quite complex and the physical environmental characteristics of the four regions are quite different, relating to their north/south orientation, their extent over three degrees of latitude, semi-enclosed nature, and their shallow bathymetry (Nunes and Lennon 1986, de Silva Samarasinghe and Lennon 1987, Bye and Kampf 2008). Both gulfs are ‘inverse’ estuaries, i.e., the salinity concentrations increase northwards away from the gulf entrances. In the northern gulfs, salinity levels are driven by evaporation rather than through gulf/shelf exchange. Also, in the northern gulfs the heat budgets are driven by surface heat exchange relating to the local arid environment and local meteorology. There are significant water temperature gradients up the gulfs, with the northern gulfs experiencing hotter summer water temperatures, but colder winter temperatures than do the waters of the southern gulfs and continental shelf. Nevertheless, despite these gradients, tidal advection and eddy diffusion tend to smooth out local, depth-related gradients (Nunes and Lennon 1986). This means that throughout large areas such as in NSG located between latitudes 33° and 34°S, water temperatures can be spatially quite uniform, except in the shallowest areas. As such, the SSTs from satellite imagery for the different broad regions that were considered are likely to have been quite indicative of those experienced by the adult Snapper during their reproductive seasons.

The SST regimes differed considerably up the two gulfs. Conforming with observations from previous studies, for NSG and NGSV the estimated monthly average SSTs were several degrees higher during summer and lower during winter compared to SSG and SGSV, respectively. Also, NSG experienced warmer summer water temperatures than did NGSV. There are gradients up the gulfs during these two extreme times of the year. Because of the seasonal gradients, the rates of change in seasonal SST must be considerably greater in the northern gulfs than the southern gulfs.

In the four South Australian regions, the pre-spawning development for some Snapper appears to commence around the same time, i.e., possibly as early as September, but then continues through October into November. There was some uncertainty about when spawning commenced because of low sample sizes throughout November. Nevertheless, in some regions spawning had commenced by mid-November, whilst by early December it had commenced in all regions. Spawning then continued throughout December until at least mid-January. For NSG, from mid-January onwards, there is little evidence of further spawning. For NGSV, the latest spawning fish were recorded on the 12th February. For both northern regions, the latest spawning fish were located in the southern parts of the regions, suggesting a gradient southward in when spawning declined. For each of SSG and SGSV, the duration over which spawning occurred continued until at least early March. These observations suggest that the variation in environmental conditions between the four regions did not necessarily influence the timing of the pre-spawning development periods and the onset of spawning but did considerably affect the durations of the spawning seasons. The tendency was that the higher the SST experienced in a region the sooner the spawning season was terminated and the more contracted was the duration of the season. For the southern regions that experienced slower rates of seasonal increase in SST to lower maxima, the durations of the spawning seasons were longer. This strongly suggests that the physiological processes involved in reproduction by Snapper were strongly influenced by the SST regimes of the different regions. This is significant as it affects the duration throughout which there is opportunity for spawning to lead to successful recruitment, an issue considered in detail in Chapter 8.

3.4.2 Seasonality of Snapper reproduction at a broader latitudinal scale

The purpose of the second component of this study was to consider the timing of reproduction at different places across a broad latitudinal range, and to compare the environmental characteristics during the pre-spawning development and spawning periods. The intention was to compare the environmental conditions during the two phases of the reproductive season to consider the environmental cues that control the two pathways in the hypothalamus-pituitary gonadal axis.

Although there were significant limitations to the data available both on the reproductive biology and environmental conditions due to the limited historical sampling that has been done, nevertheless, the study confirmed that the timing of reproductive activity for Snapper varies with latitude (Sheaves 2006, Wakefield 2006). Throughout the temperate regions of southern Western Australia, South Australia, Victoria and New Zealand, reproduction occurs during spring-summer. In contrast, in the lower latitudes in Queensland and Western Australia, the reproductive seasons are centred around mid-winter but extend from late autumn through to early spring. The season on the north coast of New South Wales was intermediate between these, involving winter to early spring. Such variable timing of reproduction is a feature that is typical for the family of Sparidae (Sheaves 2006). Comparative data amongst numerous species and genera of this family, as well as within individual species, show that spawning at lower latitudes is concentrated close to the month of lowest SST, while at higher latitudes the timing is more variable and deviates from the time of minimum SST.

The reproductive seasons for Snapper in the different places were divided into the 'pre-development' and the 'spawning' phases. Considering all places, the spawning phase corresponded with the considerable water temperature range of 15.6 to 24.4°C, which included the start and end times of the various spawning seasons when few fish would have been contributing. The range in average monthly water temperatures during the 'peak' spawning months for the temperate regions was 17-22.7°C, and for the lower latitude localities was 20-22.3°C (although there was an unexpected low in Freycinet Estuary in Shark Bay). The consequence of these different timings in reproduction between latitudes is that the products of reproduction, i.e., the eggs and larvae are exposed to a much-reduced range of environmental conditions compared to the range to which the adults are exposed throughout their distribution. This means that the peak spawning for Snapper that have lived and developed at different latitudes, occurs at relatively similar water temperature regimes. In contrast, the photoperiods during the spawning phase at the different places differed considerably with latitude. For the winter spawning in the semi-tropics, the daylength was approximately only 10 hours in duration. Alternatively, for peak spawning during summer at places such as Port Phillip Bay and the South Australian gulfs, daylength exceeded 14 hours. These results for water temperature and photoperiod suggest that the second pathway of the endocrine cascade that controls oocyte maturation through the production of luteinising hormone is controlled by a limited range in water temperature that is appropriate for egg and larval development (Pankhurst and Munday 2011).

There is empirical evidence from lab-rearing work which suggests that the water temperature range of 18-22°C is optimal with respect to the physiological tolerances of the early life history stages of Snapper. Egg rearing experiments for the sea bream *Pagrus major* (despite nomenclature issues this is considered a sub-species of *Chrysophrys auratus* (Paulin 1990, Tabata and Taniguchi 2000), involved experiments through the temperature range of 12.7 to 29.7°C. The optimum temperature range for egg survival and development was 15-22°C (Mihelakakis and Yoshimatsu 1998). Furthermore, from larval rearing experiments that compared survivorship at temperatures of 15, 18, 21, 24, 27, 30 and 33°C (Fielder et al. 2005), for all larvae in 27°C and greater, mortalities were 100%. Whilst survival rate did not vary amongst the remaining temperatures, growth rates and swim bladder inflation were low for larvae grown at 15°C. In natural conditions, low growth rates through the early life history stages are considered to increase vulnerability to predation (Houde 1987, Sogard 1997). As such, this suggests that the optimal temperature range for larval survival would be 18-24°C, but with faster growth for the higher temperatures (Fielder et al. 2005). Considering the optimal temperature ranges for both the eggs and larvae, the overlap between them identifies the optimal range for survivorship of eggs and larvae and production of viable larvae in the wild as 18-22°C (Fig. 3.5).

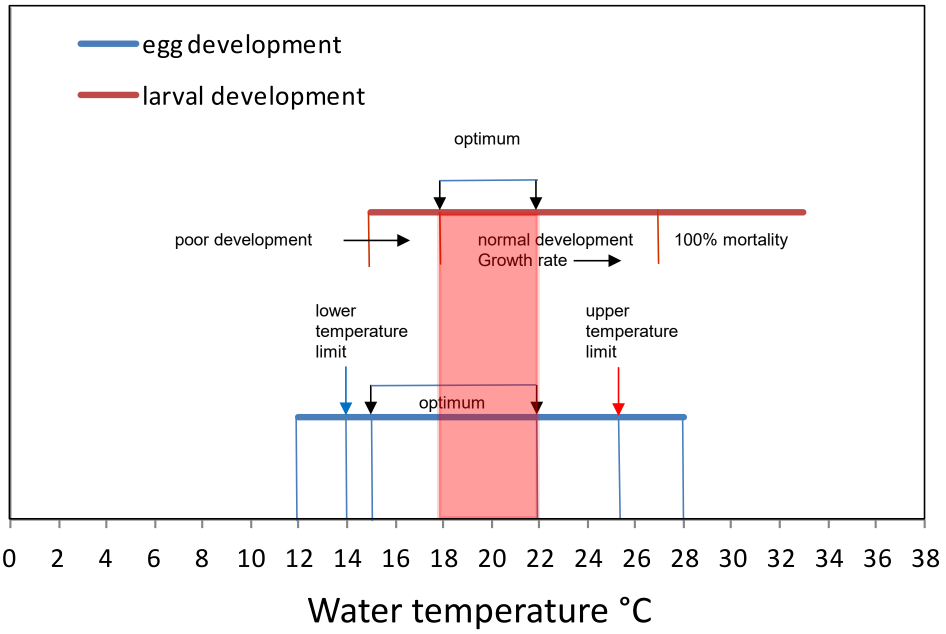


Fig. 3.5. Conceptual model showing the physiological thermal regimes of Snapper (*Chrysophrys auratus*), based on lab-rearing experiments in aquaculture facilities. The model identifies the optimal temperature regime for development throughout the early life history stages.

Although the period of 'peak' spawning in the reproductive cycle generally occurred within a limited temperature range, when compared across regions the 'pre-spawning' development phase occurred over a much broader range of environmental conditions. In south-east Queensland, pre-spawning development occurred in April and May when water temperatures declined from the high summer levels to below 26°C and daylength decreased to around 10.5 hours. In contrast, in the southern locations such as PPB, pre-spawning development occurred in early spring when water temperatures increased through the relatively low levels of 12.5 to 14.5°C and daylength increased from 11.25 to 13.5 hours. These observations suggest that the physiological processes, as controlled by the hypothalamus-pituitary gonadal axis and which culminate in gametogenesis and vitellogenesis, are stimulated by extremely different environmental conditions in different regions. Nevertheless, it is only with gonad development being initiated at such different times and under different environmental conditions is it possible for peak spawning times to occur at different places when the conditions are optimal for the survival and development of the early life history stages. Given the broad range of environmental conditions under which pre-spawning gonad development is initiated throughout the geographic range, it is difficult to nominate a single broad controlling factor. The ephemeral nature of the conditions under which pre-spawning development occurs begs the question as to whether the fish respond to different environmental cues at different places.

3.4.2 Influence of climate change

The physiological tolerance ranges of juvenile and adult Snapper are sufficiently broad for them to tolerate temperate and sub-tropical conditions. Therefore, the winter spawning of such fish suggests that the thermal requirements for gamete development or survival of gametes, eggs or larvae rather than the thermal requirements of adults determine the northern limits of their distribution. If adults can tolerate relatively high water temperatures but the early life history stages cannot, then by spawning at times of minimum temperature has enabled the species to maximise its range into the warmer latitudes (Sheaves 2006). This suggests that Snapper is a temperate species which is limited in distribution by the temperature tolerances of the early life history stages, but which has maximised its distribution through changes to the timing of reproduction.

Laboratory culture experiments have indicated that the optimal temperature range for early life history development of Snapper is 18-22°C. In natural marine environments, spawning and egg and larval survivorship do occur outside this temperature range, but in general the average monthly SST for most places for peak spawning fell within this temperature range. Consequently, to address the question about how climate change would likely affect the spawning times of Snapper might be better considered as how will the spatial regimes for SSTs in the optimal range of 18-22°C change in the future? For the eastern seaboard of Australia, there will be a general southward increase in SST regimes resulting in a southward increase in the duration of the year during which the average SST is in the range of 18-22°C. The consequence of this for Snapper is the likely displacement southward of the distribution and abundance of the species. Conditions in southeast Queensland and northern New South Wales will no longer be suitable for survival of Snapper eggs and larvae. Alternatively, the opportunity for successful spawning will increase in the open marine waters of southern New South Wales, Victoria and northern and eastern Tasmania, as well as the enclosed waters of PPB in Victoria. Projected summer temperature regimes for the northern gulfs of South Australia in the future will significantly exceed the optimal range and will be close to the lethal limits (Chapter 7). Such projected changes in regional SST regimes suggest the likelihood of significant changes in the distribution and abundance of Snapper in South Australian waters relating to poor survivorship of the early life history stages. Overall, there appears to be a high likelihood that significant changes will occur to the distribution and abundance of Snapper due to climate change, reflecting likely changes to SST regimes and their influence on the potential for survival of the early life history stages. In fact, extension of the range and increase in the abundances of Snapper in eastern Tasmania has already been evident for several years (Last et al. 2011).

3.5 References

Bye, J.A.T., Kampf, J. (2008). Physical oceanography. In: Shepherd, S.S., Bryars, S., Kirkegaard, I., Harbison, P., Jennings, J.T. (eds), Natural history of Gulf St. Vincent. Royal Society of South Australia, Adelaide, pp. 56-70.

Coutin, P.C., Cashmore, S., Sivkumuran, K.P. (1993). Assessment of the snapper fishery in Victoria. Final Report to FRDC (Project No. 1997/128). 205 pp.

Drew, M.J., Rogers, T.A., McGarvey, R., Feenstra, J., Matthews, D., Matthews, J., Earl, J., Smart, J., Noell, C., and Fowler, A.J. (2022). Snapper (*Chrysophrys auratus*) Stock Assessment Report 2022. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2007/000523-7. SARDI Research Report Series No. 1155. 178 pp.

de Silva Samarasinghe, J.R., Lennon, G.W. (1987). Hypersalinity, flushing and transient salt-wedges in a tidal gulf – an inverse estuary. Estuarine, Coastal and Shelf Science 24: 483-498.

Ferrell, D., Sumpton, W. (1998). Assessment of the fishery for snapper (*Pagrus auratus*) in Queensland and New South Wales. Final Report to FRDC (Project No. 1993/074). 143 pp.

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

Fowler, A.J., 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., Hall, K.C. (eds) (2004). Adult migration, population replenishment and geographic structure for snapper in SA. Final Report to FRDC (Project No. 2002/001). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication Number RD04/0163. 152 pp.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

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

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

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

Jackson, G., Norriss, J.V., Mackie, M.C., Hall, N.G. (2010). Spatial variation in life history characteristics of snapper (*Pagrus auratus*) within Shark Bay, Western Australia. New Zealand Journal of Marine and Freshwater Research 44: 1-15.

Lasker, R., (1985). An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*). US Department of Commerce. NOAA Technical Report NMFS 36, 99 pp.

Last, P.R., White, W.T., Gledhill, D.C., Hobday, A.J., Brown, R., Edgar, G.J., Pecl, G. (2011). Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practises. Global Ecology and Biogeography 20: 58-72.

McGlennon, D. (2003). The fisheries biology and population dynamics of Snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. PhD Thesis, University of Adelaide, Adelaide, South Australia. 212 pp.

Mihelakakis, A., 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.

Nunes, R.A., 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.

Pankhurst, N.W., Munday, P.L. (2011). Effects of climate change on fish reproduction and early life history stages. Marine and Freshwater Research 62: 1015-1026.

Pankhurst, N.W., Porter, M.J.R. (2003). Cold and dark or warm and light: variation on the theme of environmental control of reproduction. Fish Physiology and Biochemistry 28: 385-389.

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 42: 391-398.

Saunders, R.J., Fowler, A.J., Gillanders, B.M. (2012). The spawning dynamics of snapper (Chrysophrys auratus) in northern Spencer Gulf, South Australia. New Zealand Journal of Marine and Freshwater Research 46: 491-510.

Scott, S.G., 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.

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

Sogard, S.M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review.Bulletin of Marine Science 60:1129-1157.

Steer, M.A., McGarvey, R., Oxley, A., Fowler, A.J., Grammer, G., Ward, T.M., Westlake, E., Matthews, D., Matthews, J. (2017). Developing a fishery independent estimate of biomass for Snapper (*Chrysophrys auratus*). Final report to FRDC (Project No. 2014/019). 68 pp.

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

Wakefield, C.B. (2006). Latitudinal and temporal comparisons of the reproductive biology and growth of snapper, *Pagrus auratus* (Sparidae), in Western Australia. PhD thesis, Centre for Fish and Fisheries Research, Murdoch University, Perth, Western Australia.

Wakefield, C.B. (2010). Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. Journal of Fish Biology 77: 1359-1378.

Yaron, Z., Sivan, B. (2006). Reproduction. In: Evans DH, Claiborne JB (eds) The Physiology of Fishes. Taylor and Francis Group, New York. Pp 343-373.

3.6 Appendices

3.6.1 Sample sizes of Snapper for South Australian analyses of reproductive biology

Table A3.1. Summary of numbers of female Snapper sampled for their stage of reproductive development in each South Australian region across the period between 2000 and 2021.

Region	NSG	SSG	NGSV	SGSV
2000	559	196	20	47
2001	330	120	5	62
2002	185	71	2	4
2003	30	88	6	11
2004	136	11	3	52
2005	146	49	12	145
2006	166	10	115	20
2007	133	26	182	34
2008	164	238	214	90
2009	132	150	209	130
2010	113	70	99	70
2011	74	27	46	32
2012	104	14	274	58
2013	71	34	184	38
2014	87	68	62	30
2015	16	38	127	135
2016	40	6	50	111
2017	187	24	27	47
2018	11	14	126	62
2019	79	18	101	4
2020	559	137	20	11
2021	330	61	5	52
Total	2763	1470	1864	1069

3.6.2 Regional estimates of gonosomatic indices and macroscopic staging

Northern Spencer Gulf

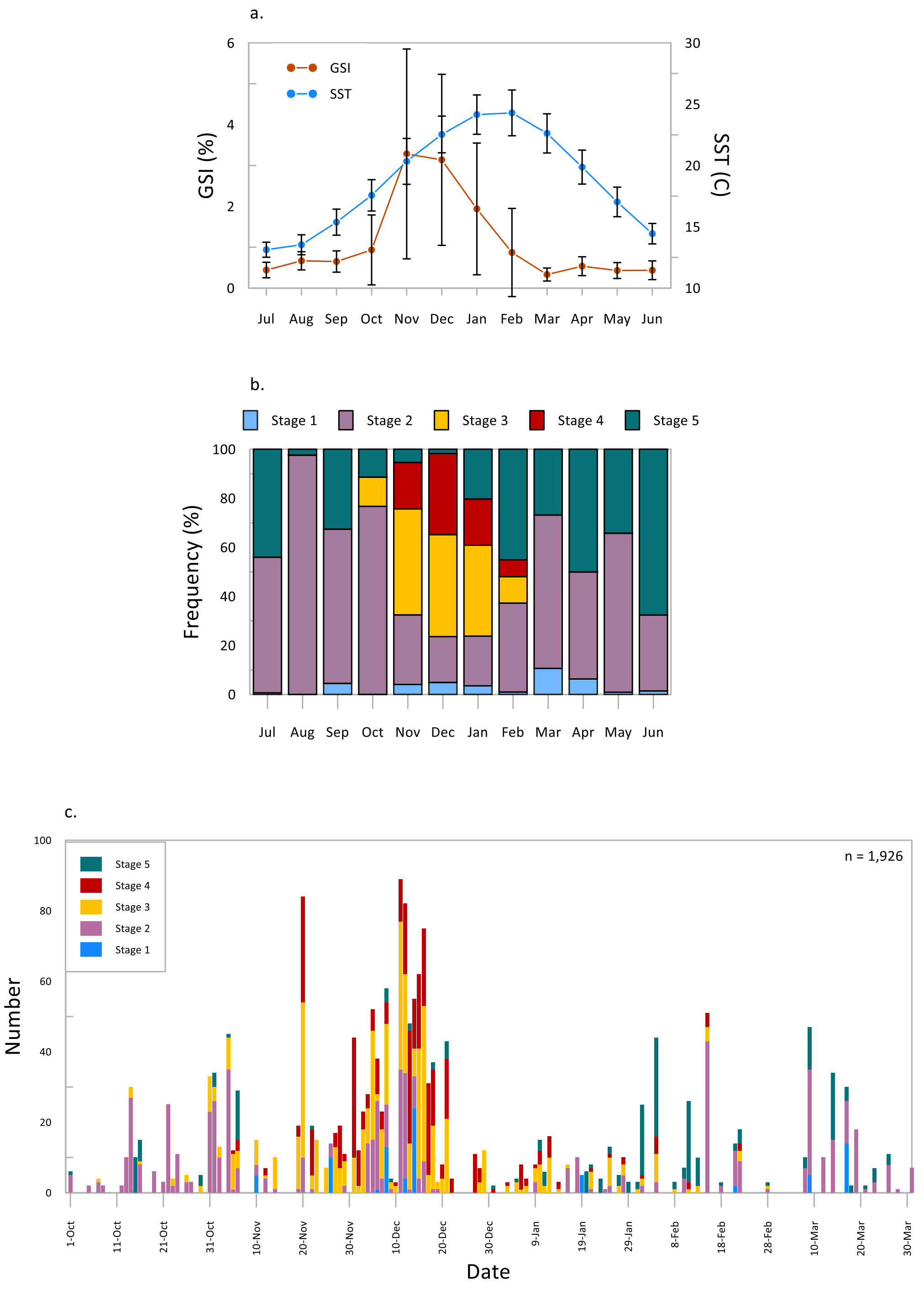


Fig. A3.1. Results from the macro analysis of Snapper ovaries from fish sampled from NSG between 2000 and 2021. a. monthly average estimates of gonosomatic indices and average monthly estimates of SST. b. summary of the macroscopic stages of ovaries. c. for all days from 1st October to 31st March, the daily totals of numbers of ovaries at the different macroscopic stages, accumulated across years.

Southern Spencer Gulf

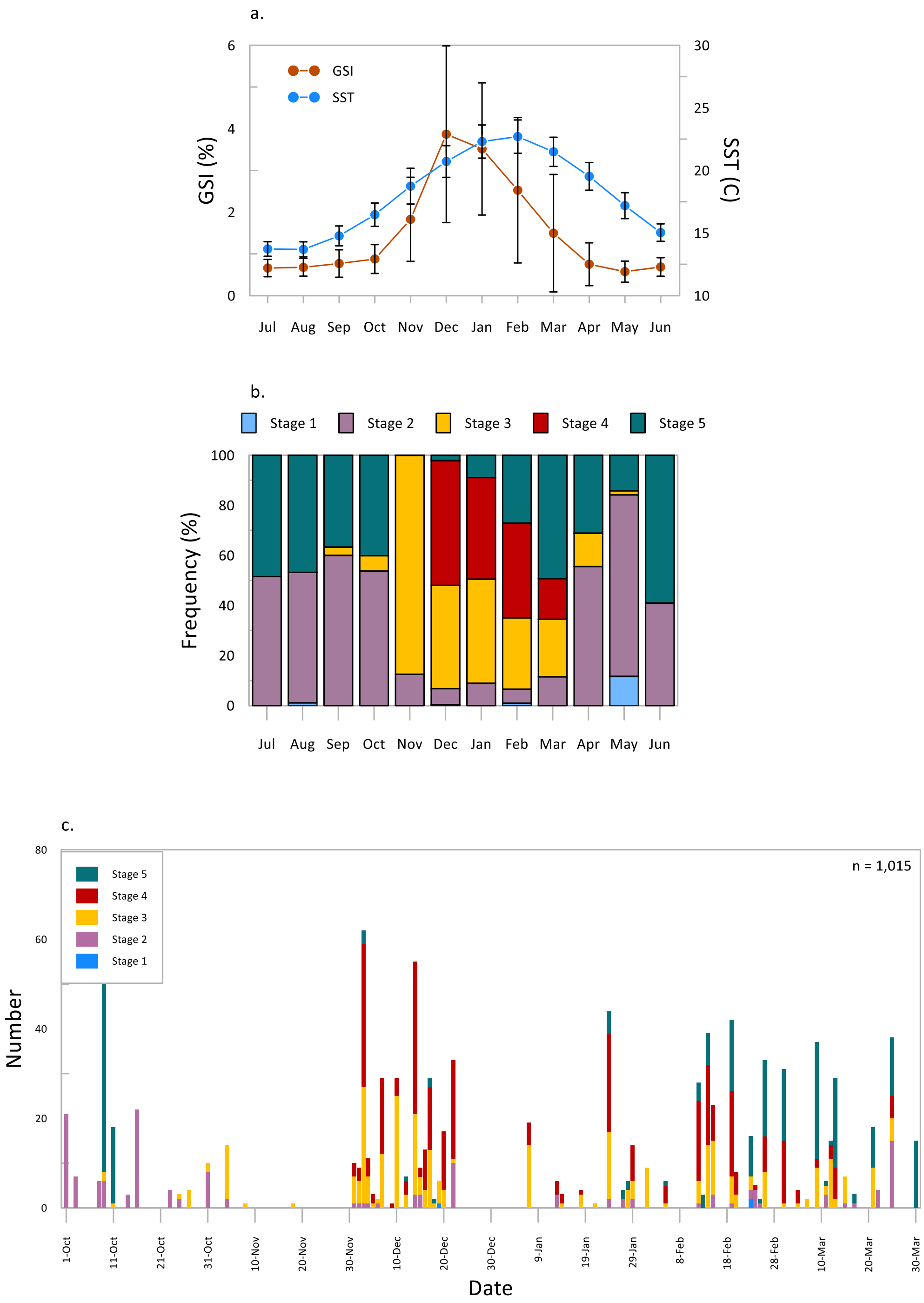


Fig. A3.2. Results from the macro analysis of Snapper ovaries from fish sampled from SSG between 2000 and 2021. a. monthly average estimates of gonosomatic indices and average monthly estimates of SST. b. summary of the macroscopic stages of ovaries. c. for all days from 1st October to 31st March, the daily totals of numbers of ovaries at the different macroscopic stages, accumulated across years.

Northern Gulf St. Vincent

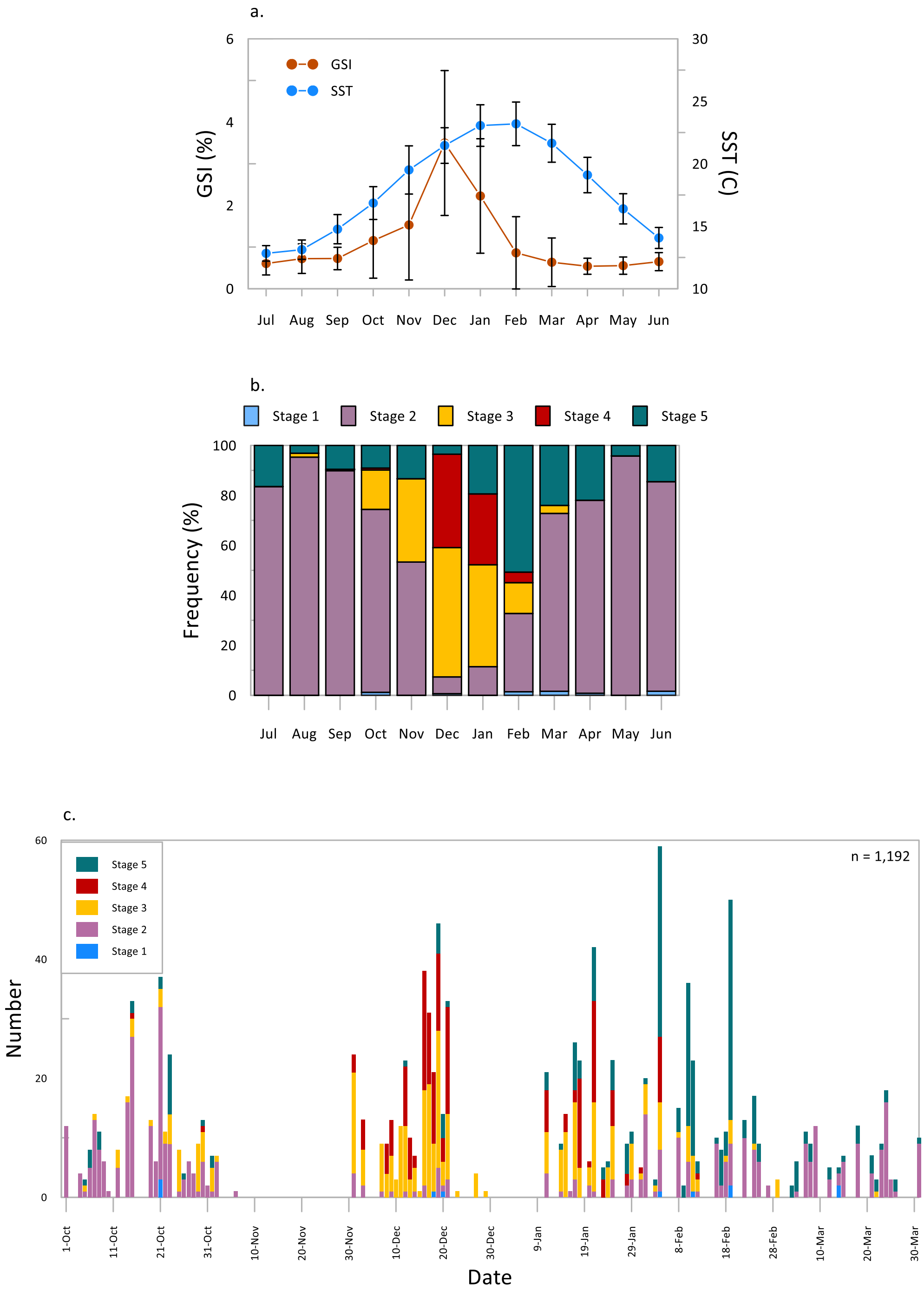


Fig. A3.3. Results from the macro analysis of Snapper ovaries from fish sampled from NGSV between 2000 and 2021. a. monthly average estimates of gonosomatic indices and average monthly estimates of SST. b. summary of the macroscopic stages of ovaries. c. for all days from 1st October to 31st March, the daily totals of numbers of ovaries at the different macroscopic stages, accumulated across years.

Southern Gulf St. Vincent

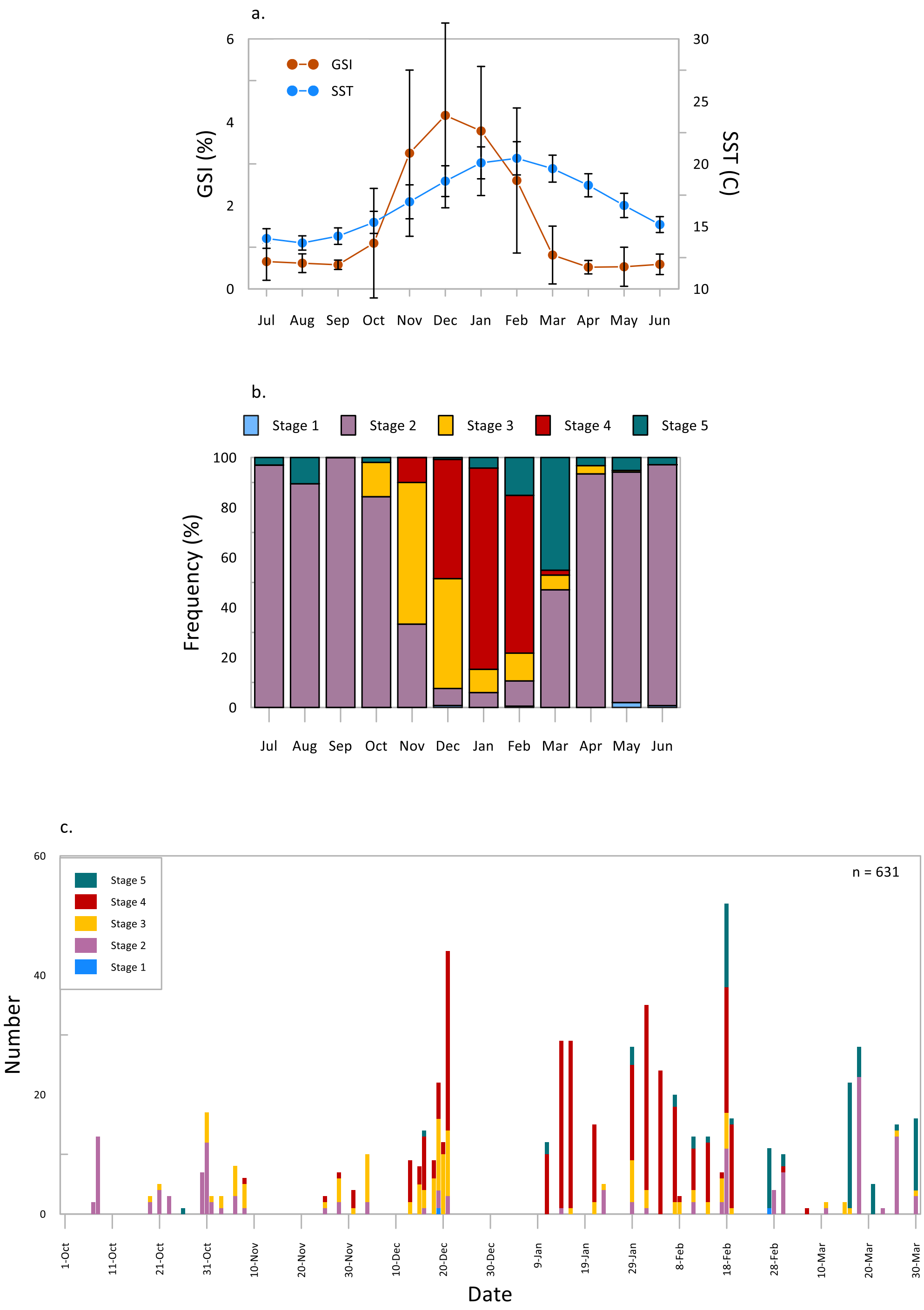


Fig. A3.4. Results from the macro analysis of Snapper ovaries from fish sampled from SGSV between 2000 and 2021. a. monthly average estimates of gonosomatic indices and average monthly estimates of SST. b. summary of the macroscopic stages of ovaries. c. for all days from 1st October to 31st March, the daily totals of numbers of ovaries at the different macroscopic stages, accumulated across years.

4. EGG DEVELOPMENT, DISTRIBUTION AND ABUNDANCE

Anthony Fowler

4.1 Introduction

Throughout the 2000s, the two main stocks of Snapper in South Australia demonstrated very different trends in fishable biomass and fishery status (Chapter 1, Fowler et al. 2020). Between 2007 and 2019, estimates of fishable biomass and recruitment for the Spencer Gulf / West Coast Stock declined to historically low levels (Fowler et al. 2020). As a result, since 2012, this regional fishery has been classified as ‘depleting’ or ‘depleted’. For the Gulf St. Vincent Stock, the 2000s has generally been a period of high biomass and exceptional fishery productivity. Nevertheless, since 2015, there have been substantial declines in fishery performance indicators. Whilst the status of this stock was classified as ‘sustainable’ until 2018, its classification was changed in 2019 to ‘depleting’ and then further downgraded to ‘depleted’ in 2020 (Chapter 1, Fowler et al. 2020). Since 2012, in response to the declining stock statuses in both gulfs, an escalating series of fishery management interventions was implemented, aimed at minimising the rate of reduction in fishable biomass and maximising the opportunity for reproductive output and recruitment (Fowler et al. 2020). These management interventions involved limiting the commercial catch, reducing recreational bag limits, and modifying seasonal and spatial closures. The management interventions culminated in the implementation of stringent fishery closures in November 2019.

Stock assessments for Snapper in South Australia have historically relied on fishery dependent data. Nevertheless, the management strategies that were implemented through the 2000s, particularly daily catch limits for commercial fishers, impacted upon the usefulness of such data as fishery performance indicators. Until then, the commercial fishery had provided a significant source of data for determining stock status (Fowler et al. 2020). As such, the determination of stock status has recently come to rely on fishery independent data, particularly estimating fishable biomass using the daily egg production method (DEPM) (Steer et al. 2017, Fowler et al. 2020, Drew et al. 2022). This method estimates the biomass of the spawning component of a fish population by empirically combining estimates of the density of the pelagic eggs of a target species with those of a range of adult parameters that relate to its reproductive biology (Lasker 1985, Steer et al. 2017).

Since the 1990s there have been several attempts to apply the DEPM for Snapper in South Australia (McGlennon 2003, Fowler et al. unpublished data, Steer et al. 2017, Fowler et al. 2020) as well as elsewhere in Australasia (Zeldis 1993, Zeldis and Francis 1998, Jackson et al. 2012). Successful application of this methodology depends on undertaking regional-scale, systematic plankton sampling, followed by accurate identification and enumeration of the Snapper eggs in the plankton samples. In South Australia, there have been several such systematic plankton sampling programs. For the first several surveys in the 1990s and early 2000s, the identification of the eggs was based solely on their morphological characteristics. However, Snapper eggs are similar in appearance to those of some other co-occurring fish species, creating ambiguity and uncertainty in their identification (Fowler pers. obs). To help circumvent these issues, in recent years a molecular biology method was developed to differentiate Snapper eggs (Oxley et al. 2017). It is based on the *in situ* hybridisation (ISH) molecular technique that uses the mitochondrial 16S ribosomal RNA gene as a target for a specific oligonucleotide probe. This probe hybridises with Snapper RNA which causes the cells of the developing embryo to turn blue, allowing the Snapper eggs to be differentiated from those of other species. This molecular technique was successfully applied in DEPMs done in 2013, 2014, 2015, 2018, 2019 and 2020. Nevertheless, despite its ability to differentiate Snapper eggs, its application for hundreds of plankton samples, can be cumbersome and time-consuming. As such, there remains a benefit to retaining the ability to identify Snapper eggs based on their morphological characteristics.

This chapter is concerned with the history of plankton surveys undertaken in South Australia up to 2020 that provided information on the distribution and abundance of Snapper eggs. It considers the morphological characteristics of Snapper eggs that can be used to differentiate them from the eggs of other species. Providing such a comprehensive description would facilitate future applications of the DEPM by helping select those eggs to be considered in the ISH process, and for circumstances under which the ISH process may not work satisfactorily (Fowler et al. 2020). There are several studies that have provided descriptions of the development of Snapper eggs (Cassie 1956, Crossland 1980, McGlennon 2003, Steer et al. 2017). Furthermore, Snapper eggs were accessed from spawning brood stock maintained at the South Australian Aquatic Sciences Centre (SAASC), for the examination of fresh and preserved material. The specific objectives addressed in this chapter were:

1. to describe Snapper eggs and their development from descriptions in the literature;
2. to identify stages in the development of Snapper eggs to which those sampled in the wild can be assigned, based on morphological characteristics;
3. and, to describe the chronology of regional plankton surveys up to 2020 that have provided information on the distribution and abundance of Snapper eggs in South Australia, comparing amongst the methods used and results obtained.

4.2 Materials and methods

4.2.1 Hatchery rearing of eggs and larvae

In 1996, brood stock of adult Snapper were captured and transported to SAASC via the MRV *Ngerin*, and were subsequently maintained at SAASC (Hutchinson pers. comm.). Through the period of 2008-10, new brood stock were added. In 2015, these fish were induced to spawn to provide eggs to assist in developing the ISH methodology. The resulting eggs were incubated at an ambient temperature of ~18-20°C, in an on-site, flow-through system. The eggs were sampled systematically, and digital images were recorded of live, ethanol- and formalin-preserved ones at different stages of development (Steer et al. 2017).

As part of the Snapper Management Science and Engagement Project Plan that was implemented in South Australia after fishery closures in November 2019, a stock enhancement program was implemented, which aimed to provide juvenile Snapper for release in each of Spencer Gulf and Gulf St. Vincent. For this project, adult brood stock in the size range of 2 to 10 kg were collected from each gulf during the summer of 2019/20. These fish were transported to, and then maintained at, the SAASC throughout 2020. Some fish from Gulf St. Vincent were induced to spawn in early October 2020 by progressively increasing the ambient water temperature to 20°C and by injecting them with hormone treatment. The resulting eggs and larvae were reared through to the juvenile stage. On a regular basis a small number of eggs and larvae were removed from rearing tanks to provide material from which to describe their development.

4.2.2 Methods for describing egg development

A general description of the characteristics of Snapper eggs is provided from the literature (Cassie 1956), enhanced by observations from hatchery-reared samples from SARDI. The characteristics considered were those that are typically used in identifying pelagic, marine fish eggs (Ahlstrom and Moser 1980), which included:

- egg size and shape;
- yolk – whether segmented or non-segmented;
- oil droplet(s) – the number, size and position of these during development;
- the chorion – whether smooth or sculptured;
- perivitelline space – the space between the yolk sac and the chorion is generally narrow but in some species is characteristically wide;
- embryonic development – state of development of the embryo, including external features, sense organs and pigmentation.

4.2.3 Plankton Sampling and Processing

Since 1994, plankton surveys have occasionally been undertaken in parts of the gulf waters of South Australia, primarily to contribute to estimating the spawning stock biomass using the DEPM. These surveys have provided quantitative information on the densities of eggs as well as their spatial patterns of dispersion. The surveys have all been based on plankton sampling from the MRV *Ngerin*, a 26 m research vessel. Nevertheless, the surveys have differed with respect to; the region, the spatial dispersion of sampling stations, their timing during the reproductive season, and the sampling methodology. Here, such information has been synthesised from various publications to provide context for considering the quantitative results.

4.3 Results

4.3.1 Snapper egg characteristics and development

Snapper eggs are spherical in shape. Whilst the size range that has been reported in the literature is from 700 to 1,000 µm, this extensive range is largely based on historic descriptions from New Zealand samples (Cassie 1956, Crossland 1980). Snapper eggs in South Australia have generally conformed to a considerably more limited size range. The sizes of eggs that were spawned in 2015 by brood stock kept at SAASC are shown in Fig. 4.1a (Steer et al. 2017), comparing between live, unpreserved eggs and some preserved in formalin. The distributions were similar and most eggs were between 820 and 920 µm with modal sizes from 840 to 870 µm.

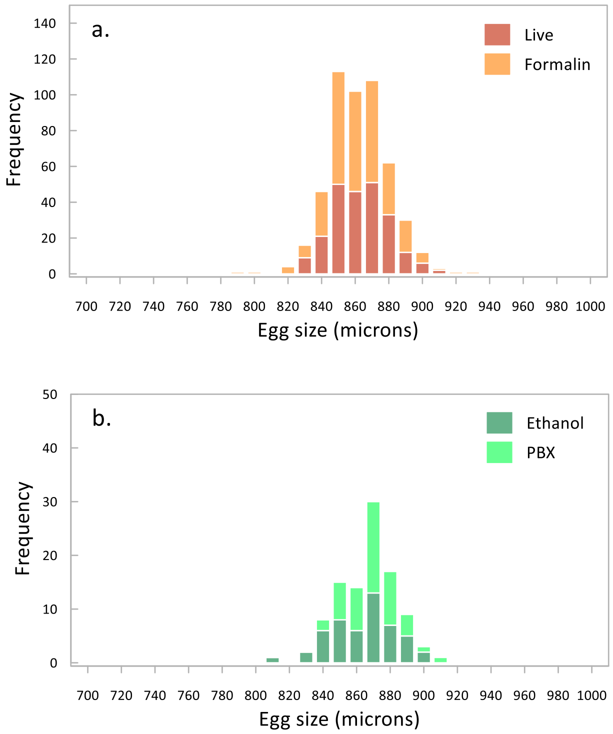


Fig. 4.1. Size distributions of Snapper eggs in South Australia. a. eggs that were spawned and reared by brood stock at SAASC, some measured live and others preserved in formalin. b. comparison of eggs from wild-caught Snapper, some preserved in ethanol and others preserved after ISH processing.

Further consideration of the sizes of Snapper eggs involved some from wild-caught fish. In early 2020, some Snapper were captured at Cape Jervis as part of the adult fish sampling program. At the time of capture, some fish were observed to have ovulated oocytes. These were then manually stripped into a bucket, mixed, and fertilized with sperm that was obtained in a similar way. The developing eggs were returned to SAASC and subsequently sampled throughout their development. These were preserved in ethanol with some subjected to ISH processing (Fig. 4.1b). The size ranges for both samples were 800 – 900 µm with modes in the range of 850 to 880 µm.

The yolk of Snapper eggs is non-segmented (Fig. 4.2). There is a single oil globule of average diameter of approximately 200 µm, which is located at the vegetal pole, opposite the blastoderm or developing embryo (Table 4.1). Later, in the newly hatched larva, the oil globule is located posteriorly in the yolk sac. The chorion of the egg is smooth and perivitelline space is narrow.

Table 4.1. Characteristics of Snapper eggs.

Characteristc	Description
Egg shape	Spherical
Egg size	Modal size ~850 – 880 µm, range ~800-900 µm
Yolk	Non-segmented
Oil globule	One, diameter for live eggs ~205 µm (± 12.6 SD)
Chorion	Smooth
Peri-vitelline space	Narrow

The following description of development of the embryo within the Snapper egg is largely based on the comprehensive description for eggs that were accessed from mature Snapper from Tiritiri Island in Hauraki Gulf, New Zealand (Cassie 1956). In that study, the sperm and eggs were manually stripped from adult fish and mixed to achieve fertilisation. The developing eggs were sampled at regular intervals until hatching occurred. The water temperature was around 18°C, to which the development times provided in the following descriptions relate. A general description of the development of pelagic marine fish eggs is provided in the Appendix 4.1.

Cassie (1956) described live, unfertilised Snapper eggs as transparent, colourless and ~0.9 mm in diameter (note that this marginally exceeds the sizes of Snapper eggs from South Australia (Table 4.1)). The **yolk** was clear and undifferentiated. There was a single **oil globule** of ~0.25 mm in diameter, which lay close to the membrane. Because of the oil globule, the eggs floated in still water. At **fertilisation**, the **perivitelline space** formed, cytoplasm differentiated from the yolk to form a circular **germinal disc** that was ~0.5-0.6 mm in diameter.

One hour after fertilisation, the first **cleavage** (cell division) occurred forming two elliptical **blastomeres**. After six hours, a series of cleavages had occurred that produced a multi-cellular, multi-layered **blastoderm** that was undifferentiated and remained at approximately the same dimensions as the original undivided germinal disc (Fig. 4.2a, 4.3a,b).

Ten hours after fertilisation, when the blastoderm was approximately 0.8 mm in diameter, the **germ ring** first appeared as a slight thickening in the deeper layer at the periphery of the blastoderm. One hour later, the germ ring was more clearly defined, and one part was beginning to spread toward the centre of the blastoderm, forming the **embryonic shield**. At 12 hours, the embryonic shield had enlarged. Furthermore, the blastoderm edge had extended toward the equator of the egg (Figs. 4.2d,e, 4.3a,b). At 13 hours, the blastoderm had spread beyond the equator of the egg, which was almost hemispherical.

After 17 hours, the blastoderm had extended and almost entirely enclosed the surface of the yolk, leaving exposed only a circular **yolk plug** of ~0.5 mm in diameter. The **embryo** appeared as a slight folding and thickening in the lower hemisphere of the egg. At 18 hours, the head had begun to take shape, but the **caudal** extremity (tail) was still little differentiated.

At 20 hours, the embryo was distinct along its length, the **optic lobes** were just beginning to appear, whilst **caudal swellings** showed prominently on either side of the posterior extremity (Fig. 4.2f). At 22 hours, the optic lobes had increased in size and the **myotomes** had begun to form, whilst the caudal swellings were no longer apparent. At 24 hours, the optic and **olfactory lobes** had become more prominent, the myotomes were more distinct and the tail extended beyond the edge of the blastoderm.

At 26 hours, the head with **visceral arches** had become more differentiated. The tail was growing away from the yolk sac and curving slightly to the right. Furthermore, the rudimentary heart could be seen just below the olfactory lobe. At 30 hours, the tail formed a rounded, blunt extremity, whilst the heart was evident as a slight projection on the ventral surface behind the head. By 39 hours, the tail had increased in length and had a more pointed tip than previously, the heartbeat was fairly regular and the embryo engaged in occasional convulsive movements.

By 45 hours, the embryo was ready to hatch (Fig. 4.2h). The eyes lacked **retinal pigment** but had a clearly differentiated lens. **Auditory capsules** occurred on either side of the posterior extremity of the head, 0.3 mm behind the centre of the eye. The tail was fully developed and terminated in a point. In these fresh, unpreserved eggs, yellow **pigment spots** were visible, particularly at the anterior and posterior edges of the eye, on both sides of the tail, whilst smaller spots occurred at intervals along the body.

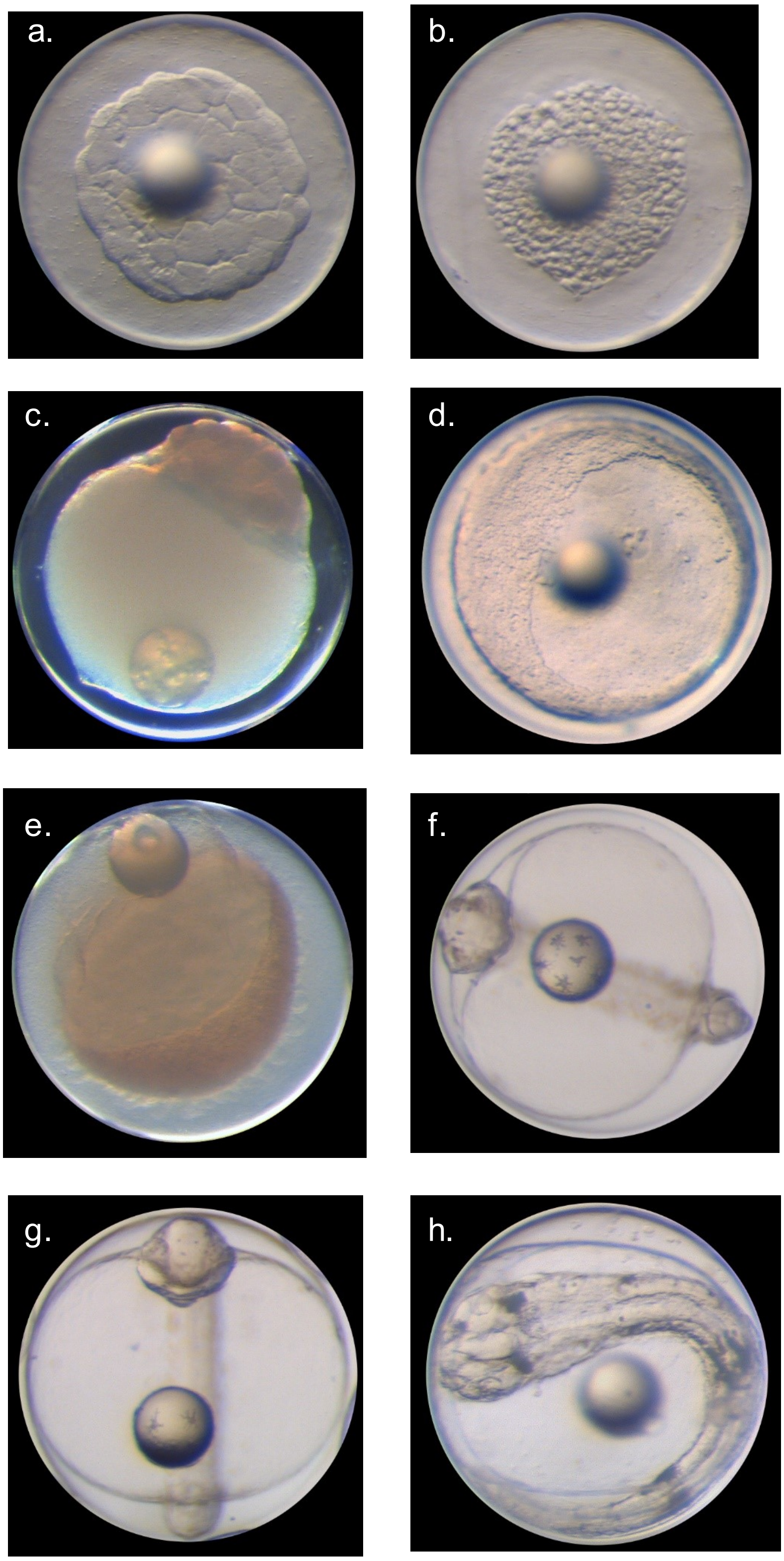


Fig. 4.2. Photomicrographs of development series for formalin-preserved Snapper eggs. a,b,c. formation of blastoderm. d,e. blastoderm edge extending past equator of egg. f,g. embryo distinct, tail bulbous and optic lobes forming. h. developed embryo prior to hatching.

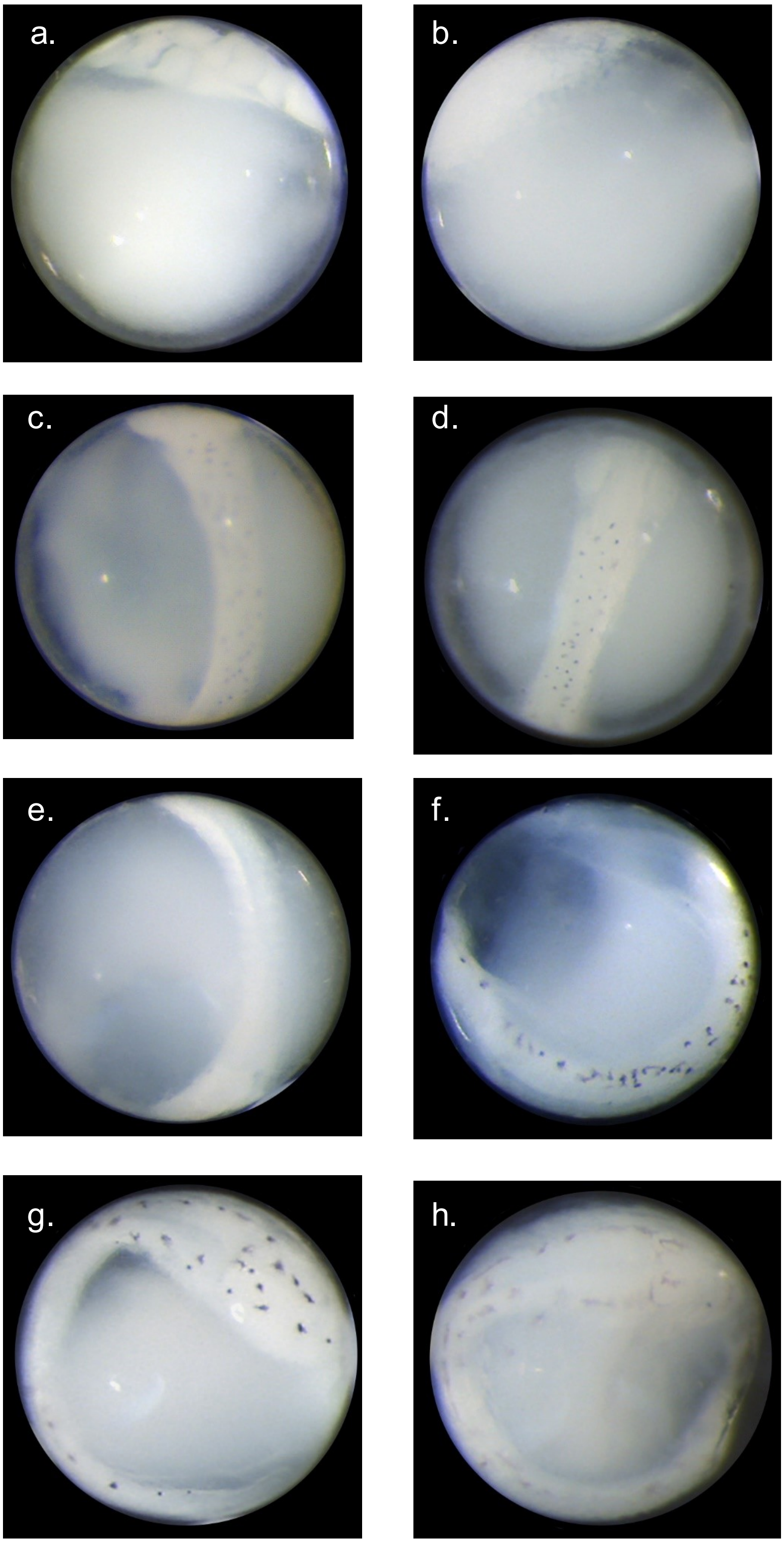


Fig. 4.3. Photomicrographs of development series for alcohol-preserved Snapper eggs. a,b. formation of blastoderm. c,d,e. embryo becoming distinct. f. melanophores developing along length of embryo. g,h. developed embryo with stellate, non-uniform melanophores, with clear patch behind the head.

4.3.3 Developmental staging and egg ageing

For DEPM applications it is necessary to identify Snapper eggs from plankton samples and to assign them to a stage of development (Steer et al. 2017). From the development sequence summarised above from the descriptions of Cassie (1956), different authors have identified different stages of development. Recent applications of the DEPM in South Australia used a nine-stage system (Steer et al. 2017), derived from the 16-stage system that was developed by McGlennon (2003) from descriptions by Crossland (1980). The comparison between the classification system developed by McGlennon (2003) and that used by Steer et al. (2017) is presented in Table 4.2.

Table 4.2. Descriptions of development stages for Snapper eggs comparing between those used by McGlennon (2003) and Steer et al. (2017).

Stage	Description – McGlennon (2003)	Stage	Description Steer et al. (2017)
1	up to 16 cells		
2	>16 cells but individual cells visible	I	<64 cells. Individual cells are discernible in live eggs, but have a rough ‘bubbled’ appearance when preserved in ethanol and formalin
3	individual cells indistinguishable but prior to epiboly		
4	blastodisc starting to enlarge at periphery of blastodisc	II	blastoderm covers less than half the yolk
5	blastodisc covers about 1/3 of yolk, germ ring starting to thicken		
6	blastodisc covers about ½ yolk, germ ring distinct	III	blastoderm covers more than half the yolk, becoming hemispherical. The blastopore is not yet formed
7	blastodisc covers about ¾ yolk, gastrulation commenced, embryo visible		
8	embryo reaches 2/5 around yolk with rudimentary head, blastopore small adjacent to caudal region	IV	blastopore apparent, the embryonic axis forms, and the head becomes distinct
9	blastopore closed, optic vesicles visible, tail formed	V	blastopore is closed, optical vesicles visible, first myomeres visible, sparse pigment spots on the dorsal and ventral surfaces of the embryo
10	embryo reaches <50% around yolk, first myotomes visible centrally, tail flat		
11	embryo reaches to 50% of yolk, optical vesicles are clear	VI	embryo extends 50% around the yolk. Tail becomes bulbous and begins to separate from yolk. Pigment appears on oil globule (as stellate melanophores) and becomes more prominent on the embryo and yolk sac.
12	embryo reaches to >50% of yolk, tail thickened at base		
13	tail lifted from yolk at base, embryo straight	VII	embryo extends 66% around yolk. Tail lifts from yolk and extends to oil globule. Caudal finfold begins to develop. Melanophores appear more prominent at anterior end of embryo
14	tail with some curvature		
15	embryo reaches to >75% of yolk, finfold evident around tail, oil globule still central	VIII	embryo extends 75% around yolk. Head structure and caudal finfold are well developed, Tail extends beyond oil globule
16	long tail, oil globule ventral in yolk sac	IX	embryo is almost fully developed, tail long and twisted off embryo axis. Oil globule is posteriorly located near anus.

Note that the multi-stage system developed by McGlennon (2003) and the early descriptions of Cassie (1956) and Crossland (1980) provide little mention of the pigmentation on the embryo or the oil globule in the developing egg. In contrast, these were important features considered by Steer et al (2017). Pigment spots are included in their descriptions of eggs from Stage V onwards. The following observations were made during a conversation with Gretchen Grammer in March 2022:

i. the melanophores in live embryos can change shape between stellate, round and disc-shaped. So, depending on the state the melanophores were in when the eggs were preserved determines their appearance when being sorted and identified;

ii. if plankton samples were preserved and then refrigerated, the melanophores can have dark colouration. Alternatively, if the samples were not refrigerated, they can be reddish in colouration. If Snapper eggs are examined live, the melanophores can appear yellow (as described by Cassie 1956).

Following is a description of the development of Snapper eggs that conforms to the terminology used for the stages of development described by Steer et al. (2017) (Table 4.2) and relates to the photographs presented in Fig. 4.4. The eggs were spawned and reared at SAASC in November 2015 and preserved in formalin.

Cleavage and formation of the blastoderm occur within the first few hours after fertilisation (Fig. 4.4a,b). After the blastoderm has extended to cover half the yolk, the embryonic axis forms and the head becomes distinct (Fig. 4.4c). Then the optical vesicles form (Fig. 4.4d). When the embryo extends 50% around the yolk, the tail becomes bulbous and begins to separate from the yolk. Furthermore, pigment appears on the embryo and oil globule as reddish, stellate melanophores (Fig. 4.4e), which become more distinct as the embryo develops (Fig. 4.4f). Eventually, the tail becomes pointed and twists off the mid-line of the egg (Fig. 4.4g). After hatching there are distinct reddish melanophores along the dorsal surface of the embryo and the oil globule, which is located posteriorly in the yolk sac (Fig. 4.4g).

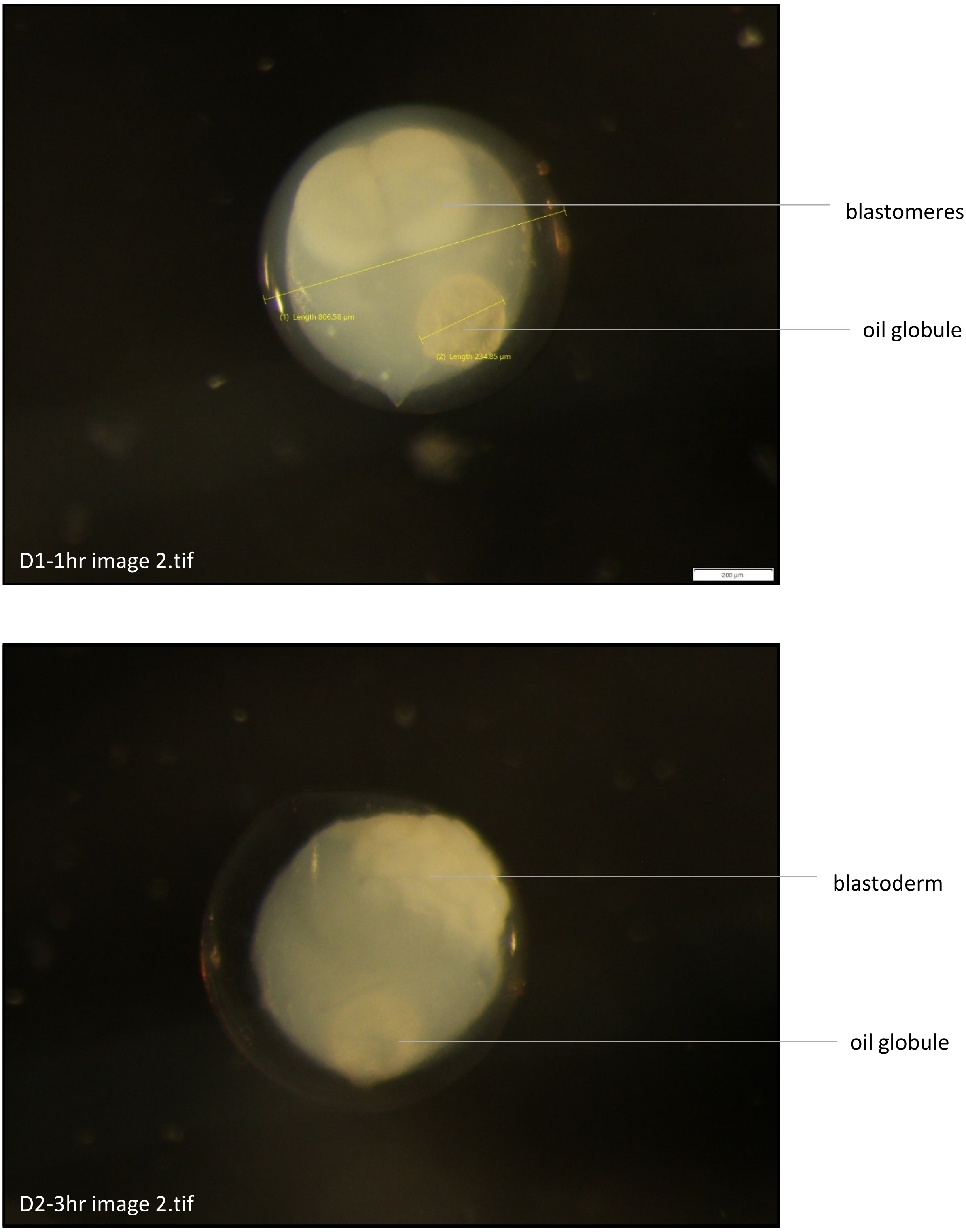
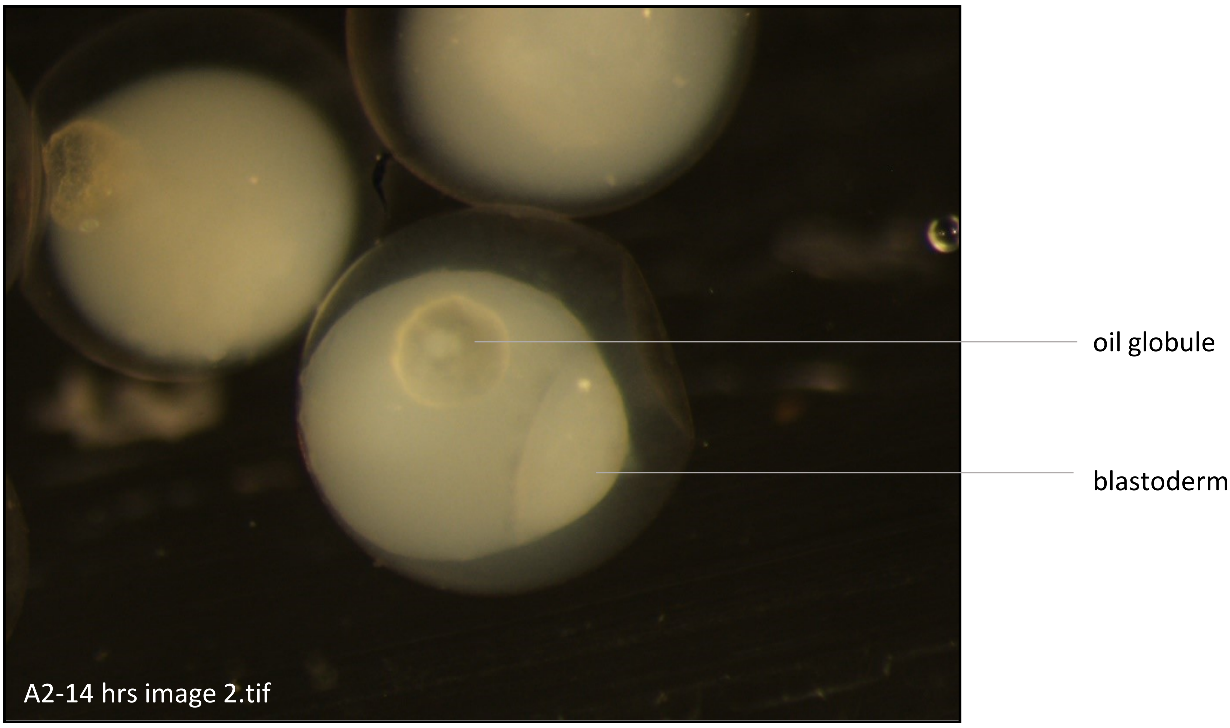


Fig. 4.4a. Early development of Snapper eggs. Top – early cleavage resulting in production of four blastomeres after one hour. Bottom – multi-cellular, multi-layered blastoderm after three hours.



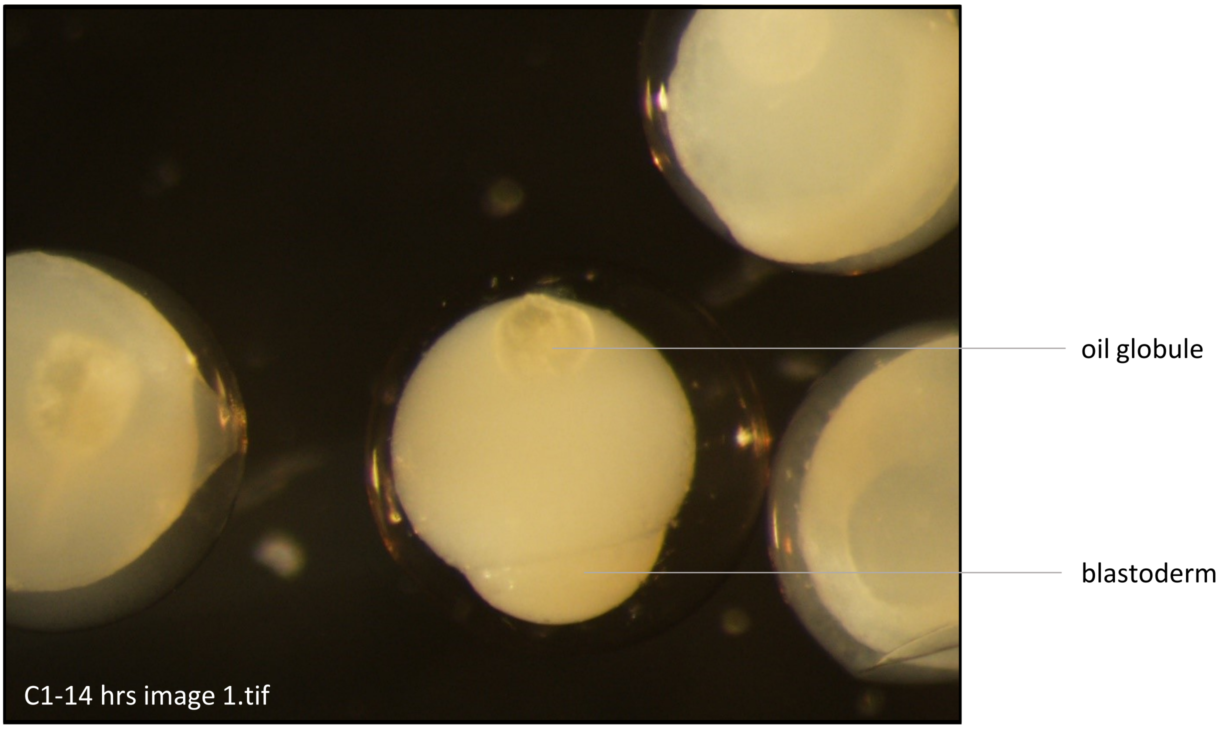
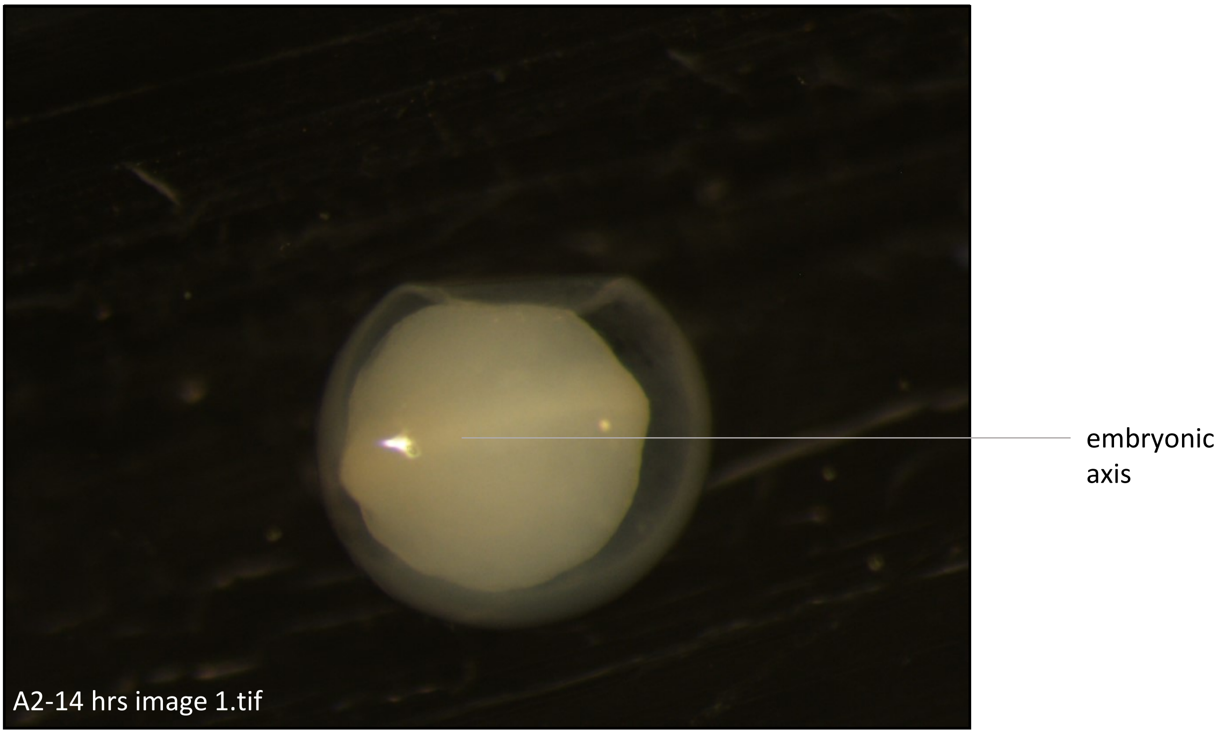


Fig. 4.4b. Development of Snapper eggs after 14 hours. Top – multi-cellular, multi-layered blastoderm. Bottom – multi-cellular, multi-layered blastoderm.



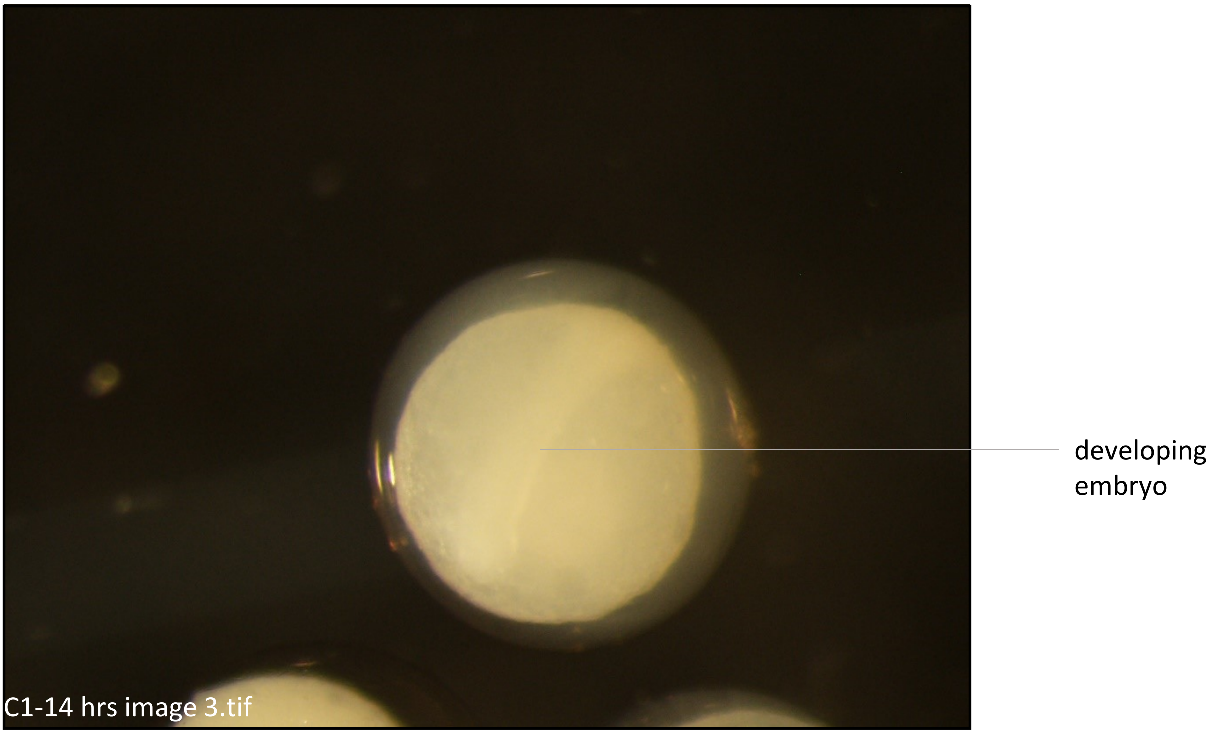
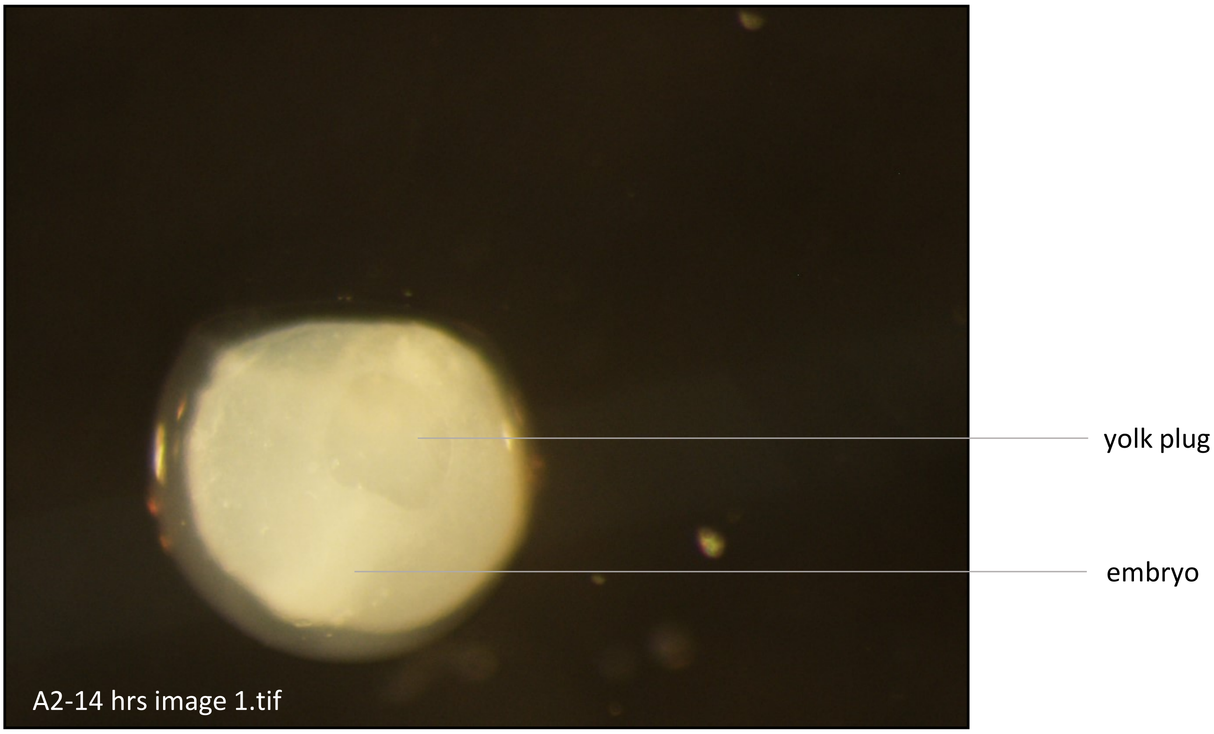


Fig. 4.4c. Development series for Snapper eggs after 14 hours. Top - dorsal view of the recently formed embryonic shield. Bottom – dorsal view of the developing embryo.



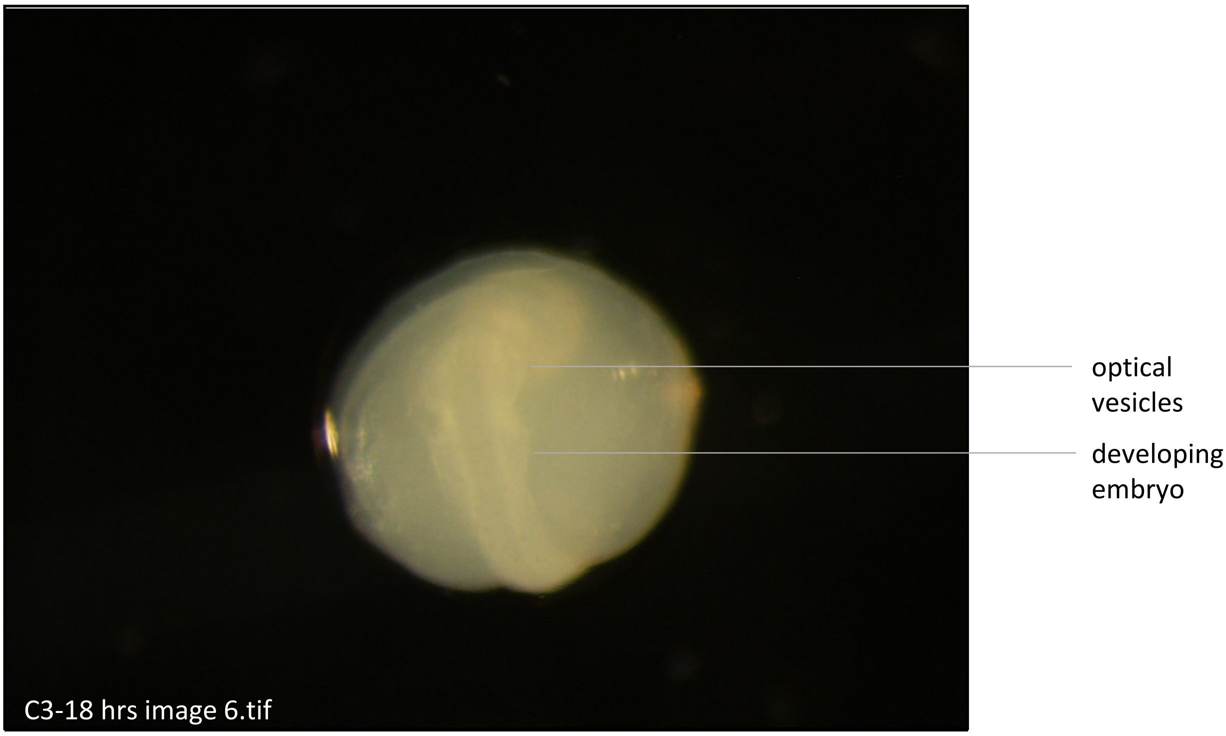


Fig. 4.4d. Development series for Snapper eggs after 14 hours. Top - ventral view of the yolk plug centrally located as well as the head and tail of the embryo. Bottom – dorsal view of the developing embryo showing recently formed head.

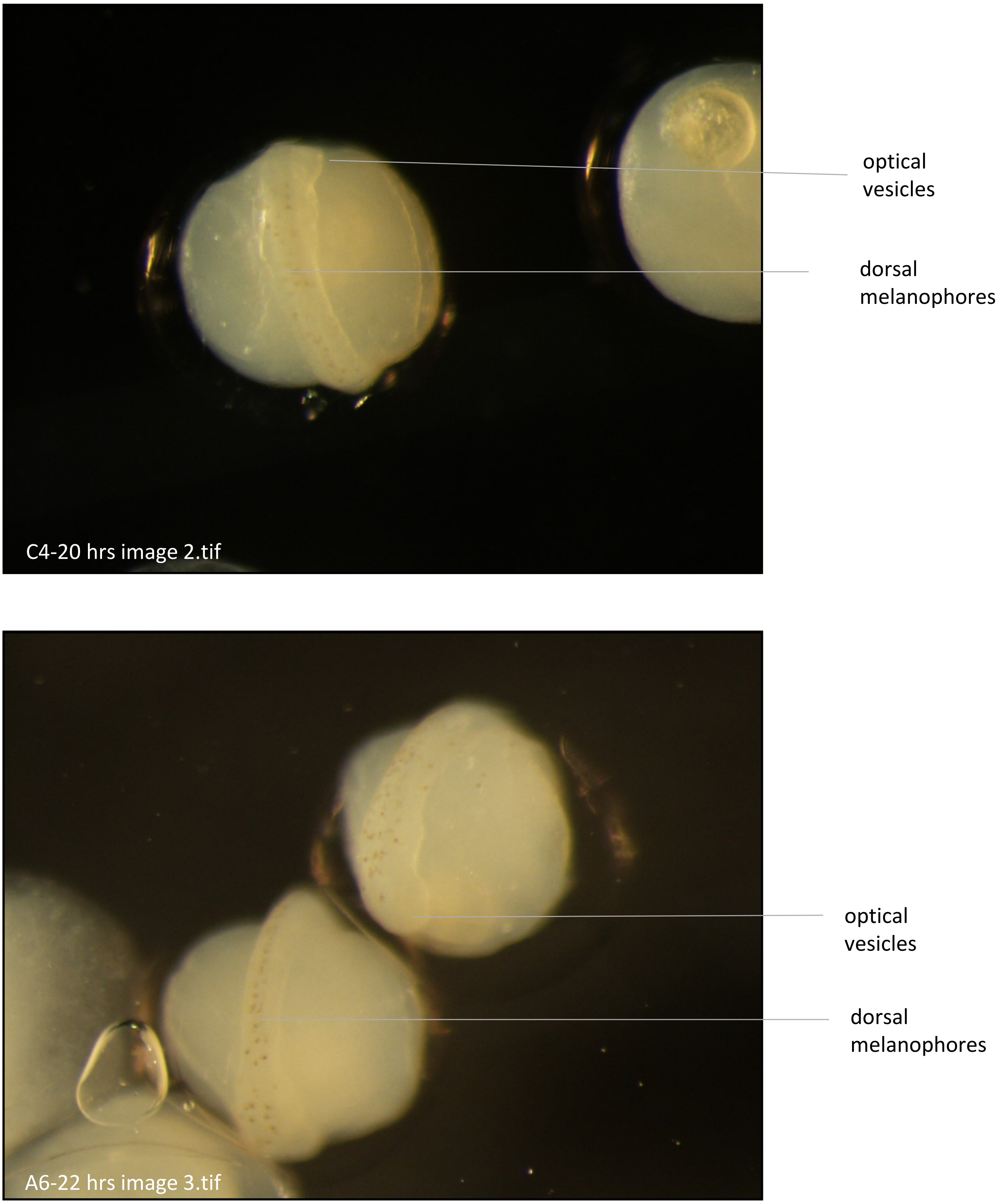


Fig. 4.4e. Development series for Snapper eggs after 20 - 22 hours. Top - dorsal view of the head and trunk of embryo showing melanophores dotted along the body length. Bottom – the melanophores on the head and trunk are reddish and stellate in shape.

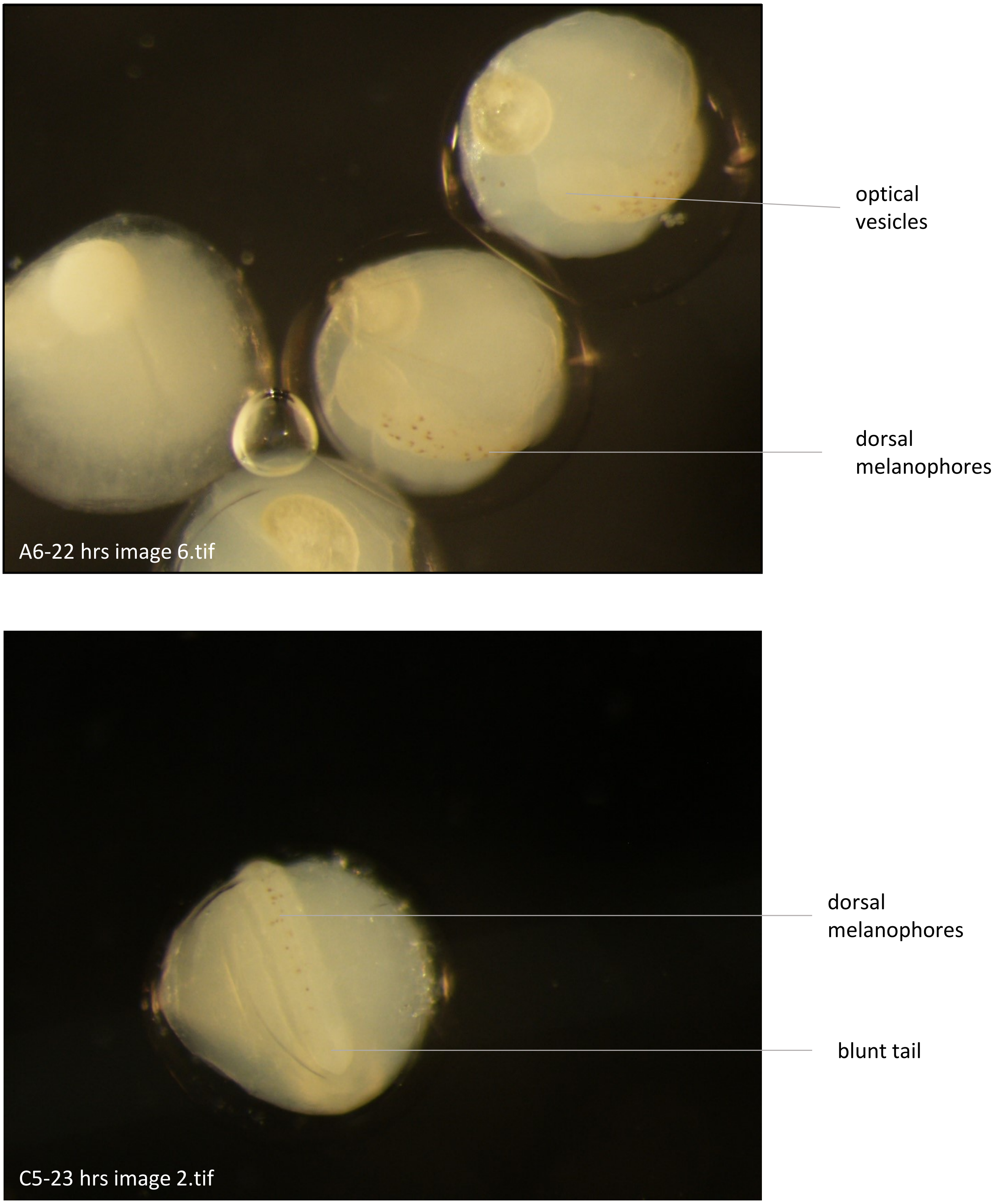
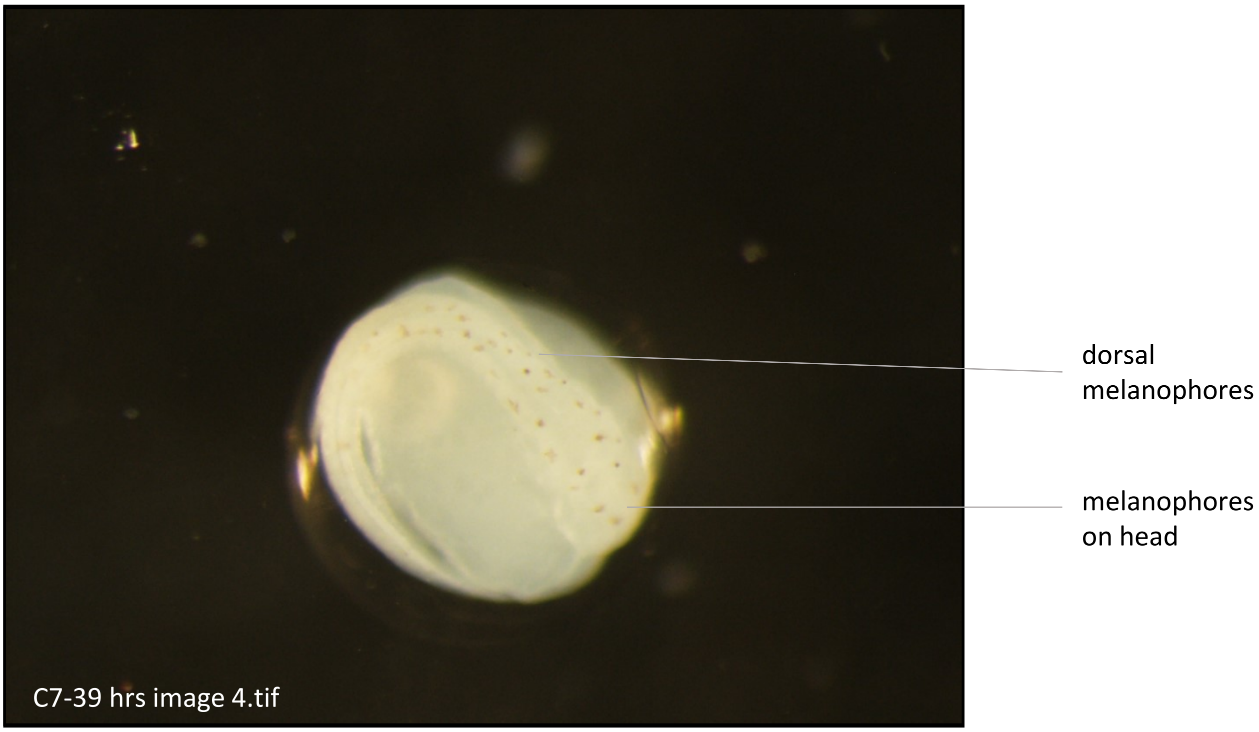


Fig. 4.4f. Development series for Snapper eggs after 22 - 23 hours. Top – melanophores are located on the head and along the length of the trunk. Embryo still located along mid-line of the yolk. Bottom – blunt tail still lies along mid-line of the yolk.



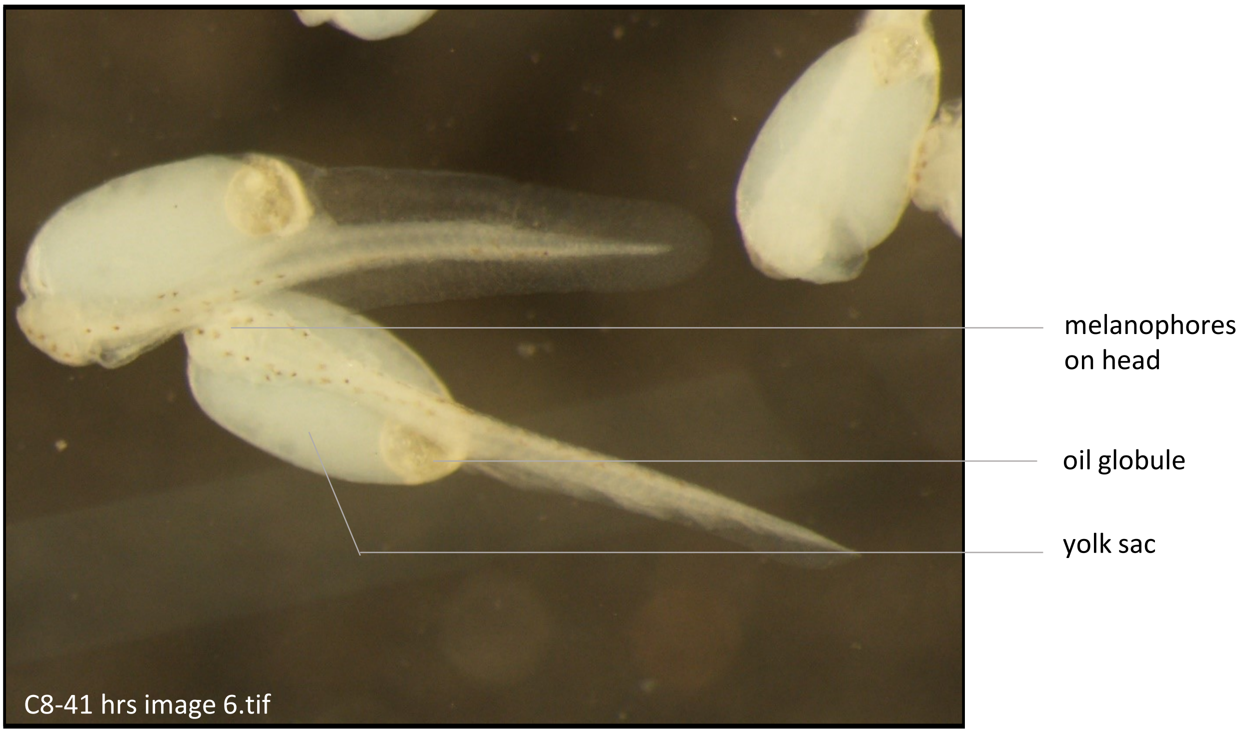


Fig. 4.4g. Development series for Snapper eggs prior to and after hatching. Top – melanophores are located on the head and along the length of the trunk. Tail of the embryo demonstrates flexure away from the mid-line. Bottom – newly hatched larvae showing the distribution of reddish melanophores on the head and along the trunk, as well as the posterior-located oil globule.

4.3.4 Chronology of Snapper egg surveys in South Australia

1994 - 1996

The first plankton surveys that targeted Snapper eggs in South Australia were done throughout the mid-1990s and were focussed on Northern Spencer Gulf (NSG) (McGlennon 2003). Sampling was done during each of November and December 1994 and then in December 1995 and January 1996. These surveys were done from the MRV *Ngerin* using paired plankton nets of 70 cm diameter and 3 m in length. For the first cruise, one net had 500 µm mesh and the other 363 µm mesh. After November 1994, only 500 µm mesh nets were used. At each station, flowmeters (General Oceanics R) were used, one in each net, to measure transect length and to calculate volume of water sampled. Sampling was done along 15 east-west transects that were located along lines of latitude that were 15 nm apart with sampling stations located evenly along transects. Oblique tows of the nets were done from the seabed to the surface. Such sampling was generally done between 12:00 and 24:00 hours each day (Table 4.3). The plankton samples were preserved and stored in a 5% formalin seawater solution in 1 L plastic containers.

In the laboratory, the plankton samples were sorted using a glass Z-tray and a binocular microscope at x100-160 magnification. To facilitate plankton sorting, the samples were sub-sampled as required, depending on the quantity of plankton. The Snapper eggs were removed, counted, and assigned to one of 16 development stages (Table 4.2). When sub-sampling occurred, the counts of Snapper eggs were multiplied by the inverse of the sample fraction to estimate the total number of Snapper eggs caught at each station, which was then converted to an estimate of density (d_{ij} = no. of eggs.m^{-2} surface area):

$d_{ij} = n_{ij}*(de_j/v_j)$

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

de_j = depth sampled at station j (m)

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

December 2000

This Snapper egg survey was undertaken in NSG as part of a further attempt to estimate spawning biomass using the DEPM (Fowler pers. comm.). At that time, this region was the focus of South Australia's Snapper fishery, having for the preceding 16 years dominated the State's commercial catches (Fowler 2002). The geographic area sampled was the same as that considered by McGlennon (2003), and the sampling was done along similar transects. However, the sample stations along the east-west transects were 5 nm apart, which resulted in a total of 75 stations being sampled (Table 4.3). Plankton sampling was primarily done during the day between 06:30 and 19:00 hours. At each station, an oblique plankton tow was done using double bongo nets. Both nets were 70 cm in diameter and had 500 µm mesh. Flowmeter readings were recorded to be later used to estimate transect length and volume of water sampled. The plankton samples were preserved in 5-10% formalin seawater solution. Later, in the lab, the fish eggs were removed, and Snapper eggs were identified based on morphological characteristics.

2013 - 2015

In 2013, 2014 and 2015, Snapper egg surveys were undertaken to again assess the usefulness of DEPM for estimating the spawning biomass of Snapper. This was done as part of FRDC Project 2014/019 that was aimed at developing a fishery-independent method for assessing Snapper stocks (Steer et al. 2017). NSG was once again considered. In 2013, the area surveyed was marginally larger than that considered during the 1990s and 2000. In 2015, the survey area was extended southward. Also, plankton surveys were undertaken throughout Gulf St. Vincent (GSV) and Investigator Strait (IS). Either one or both gulfs were sampled in each of the three years (Table 4.3). For each regional survey, the plankton sampling was done from the MRV *Ngerin* using paired bongo nets with 500 µm mesh, mounted on a steel frame. The nets were deployed vertically from the side of the vessel. They were lowered to within 5 m of the seabed and then slowly retrieved at ~1m.sec^{-1}. A General Oceanics TM 2030 flowmeter was mounted in the mouth of each net. For each deployment, their readings were used to measure the distance travelled by the nets, whilst the wire length during each deployment was measured to the nearest metre using a digital counter (General Oceanics). When retrieved, the nets were washed down, and the plankton captured in both cod-ends was rinsed into a single 1 L container. In 2013 and 2014, ethanol (95%) was used as a preservative. However, in 2015, when it was thought that egg identification would need to be done based on morphological characteristics, most samples were preserved in 5% buffered seawater formalin, and only every fifth sample was preserved in 95% ethanol (Steer et al. 2017).

Table 4.3. Details of Snapper eggs surveys undertaken in South Australia for the purpose of estimating total egg production for application of the DEPM methodology.

Region	Month / Year	Number of stations sampled	Dates of sampling	Plankton tow type
NSG	Nov 1994	36		Oblique
NSG	Dec 1994	38	13-16 Dec	Oblique
NSG	Dec 1995	38	12-15 Dec	Oblique
NSG	Jan 1996	36	13-16 Jan	Oblique
NSG	Dec 2000	75	12-17 Dec	Oblique
NSG	Dec 2013	188	11-15 Dec	Vertical
NSG	Dec 2015	212	2-6 Dec	Vertical
NSG	Dec 2018	191	10-16 Dec	Oblique
NSG	Dec 2019	272	5-11 Dec	Oblique
GSV/IS	Dec 2014	216	11-16 Dec	Vertical
GSV/IS	Dec 2015	202	7-11 Dec	Vertical
GSV/IS	Dec 2018	176	17-19 Dec	Oblique
GSV/IS	Jan 2020	265	13-19 Jan	Oblique

2018 - 2020

From 2018 to 2020, further Snapper egg surveys were undertaken throughout both NSG and GSV/IS as part of DEPMs to provide estimates of spawning biomass to contribute to stock assessments (Fowler et al. 2019, 2020). For these plankton surveys, the sample areas considered were larger than those considered in 2013 and 2015. Furthermore, there was a significant change to the sampling methodology. Instead of the paired bongo nets being deployed vertically, oblique tows were done to increase the volume of water that was sampled per station to maximise the possibility of catching Snapper eggs (Table 4.3). For these oblique tows, the nets were deployed over the stern of the vessel. The cable to which the net frame was attached was allowed to run out as the vessel proceeded forward at <4 kn. As the net frame was weighted with a heavy paravane, the net mouth was kept open and facing forward, which allowed it to sample as it submerged and as it was retrieved to the surface. The net was lowered to within 5 m of the bottom and subsequently retrieved by winching in at an angle of ~45°, with the vessel in neutral during retrieval. The tide and wind conditions determined the distance travelled and volume of water sampled at different stations. The latter was estimated based on flowmeter readings.

After each plankton survey undertaken between 2013 and 2020, the plankton samples were removed to the SAASC and processed over the following months. This involved the detailed examination of the plankton from each station using a dissection microscope during which the fish eggs were removed. At this time, the latter were divided into ‘possible’ and ‘unlikely’ Snapper eggs, based on their sizes and morphological characteristics. Later, for the ‘possibles’, the molecular biology approach, which involved the application of the *in situ* hybridization (ISH) molecular technique that uses the mitochondrial 16S ribosomal RNA gene as a target for a specific oligonucleotide probe (Steer et al. 2017), was used to identify the Snapper eggs.

For the fish eggs from the plankton samples collected in NSG in December 2019 and GSV/IS in January 2020, the hybridization of Snapper eggs during the ISH processing was less pronounced than for previous assessments (Steer et al. 2017; Fowler et al 2019). For these samples, the identification of Snapper eggs largely depended on morphological characteristics from the descriptions provided above.

Comparison of results amongst years

The information that is now available from the plankton sampling done during the 1990s is limited as it was not possible to locate electronic versions of the original data files, although there was some limited information in hard copy (provided by D McGlennon). There were no data for the sampling done during November 1994. For December 1994, only the spatial data with respect to locations of sampling stations as well as the physical environmental data were available. The biological information for the numbers or densities of Snapper eggs in hard copy were ambiguous.

For December 1995 and January 1996, the spatial information, physical environmental data and raw counts of Snapper eggs were available for each station. However, the flowmeter readings were not available, which prevented calculating the linear distances and volumes of water sampled. The estimates of egg density were presented figuratively by McGlennon (2003). These comparative maps indicated that more Snapper eggs were captured in December 1994 than the previous month and were predominantly found in the mid-region between Wallaroo and Wood Point.

For December 1995 and January 1996, there were estimates available of the numbers of Snapper eggs captured at the different stations. For the former period, an estimated total of 2,672 Snapper eggs was captured from the two nets at 38 stations (excluding two where only one net was considered). The eggs were predominantly located in the mid-region between Cowell and Port Pirie, with very few captured south or north of these lines of latitude, respectively (McGlennon 2003). Whilst the average catch was ~70 eggs.station^{-1} (Table 4.4), two stations were particularly significant. One station located off Cowell produced a density of ~40.m^{-2}, whilst the station located off Wood Point produced an estimated 1,328 Snapper eggs at a density of 83 eggs.m^{-2} (McGlennon 2003). In January 1996, an estimated 432 Snapper eggs were captured, considerably fewer than in December 1995. These were broadly distributed between Cowell and Whyalla. At most stations no Snapper eggs were captured, whilst at three stations there were >100 Snapper eggs and at several others there were up to 20 eggs.

In 2000, a total of 75 stations was sampled, which was considerably lower than the numbers sampled during the 2000s (Table 4.4). Nevertheless, the total distance and volume of water sampled were both relatively high, reflecting long transect lengths and the larger diameter of the nets used. So, although a relatively high number of Snapper eggs were captured, this translated to the moderate average density of 34.0 Snapper eggs.1000m^{-3}. The eggs were again patchily distributed throughout the study area, although none were captured from Port Pirie northwards.

In 2013 and 2015, NSG was sampled using vertical plankton tows. In both years, this severely limited the transect length at each station, which meant that overall, the total distance and volume of water sampled were very low (Table 4.4) (Steer et al. 2017). Low numbers of fish eggs were captured, which included relatively few Snapper eggs. These were found at <15% of the sample stations. Despite that the eggs were patchily dispersed they were broadly distributed from Point Lowly in the north to Cape Elizabeth in the south (Fig. 6 in Steer et al. 2017). For GSV/IS, the vertical plankton tows undertaken in 2014 and 2015 also sampled a relatively short distance and low volume of water (Table 4.4). Relatively few Snapper eggs were captured that were distributed across only <15% of the stations sampled. Nevertheless, these stations were distributed throughout the whole region from NGSV to the western extent of IS (Fig. 6 in Steer et al. 2017).

Table 4.4. Details of results from Snapper egg surveys undertaken in South Australia between the 1990s and late 2000s.

Region	Year	No. stations	Total distance sampled (m)	Total volume sampled (m^{3})	No. stations with Snapper eggs (%)	Total fish eggs	No. Snapper eggs	Snapper eggs per station	Density No.1000m^{-3}
NSG	Nov 1994	36			23 (60.5)				
NSG	Dec 1994	38			32 (84.2)				
NSG	Dec 1995	38			16 (42.1)		2,672	70.32	
NSG	Jan 1996	36			14 (38.9)		432	12.0	
NSG	2000	75	35,946	27,667	41 (54.7)		941	12.54	34.0
NSG	2013	188	4,182	2,134	26 (13.8)	31,909	81	0.43	38.0
NSG	2015	212	4,308	2,198	20 (9.4)	18,911	30	0.14	13.6
NSG	2018	191	28,325	14,448	156 (81.7)	69,668	1,204	6.30	83.3
NSG	2019	272	34,505	17,601	97 (35.7)	164,822	223	0.82	12.7
GSV/IS	2014	216	5,021	2,561	31 (14.4)	12,425	73	0.34	28.5
GSV/IS	2015	202	5,561	2,838	24 (11.9)	15,340	36	0.17	12.7
GSV/IS	2018	138	20,930	10,676	111 (80.4)	31,703	1,222	8.86	114.5
GSV/IS	2020	265	43,527	22,203	173 (65.3)	115,449	1,586	5.98	71.4

In NSG in 2018 and 2019, oblique plankton tows were used at high numbers of sample stations. These surveys resulted in long total distances and large volumes of water sampled and relatively high numbers of fish eggs captured (Table 4.4). There was a relatively high number of Snapper eggs captured in 2018, which produced the high density of 83.3 eggs.1000^{-3}. The eggs were broadly distributed throughout the whole region and were generally evenly dispersed compared to previous surveys (Fig. 4-16 in Fowler et al. 2019). In 2019, despite a considerably larger number of fish eggs, far fewer Snapper eggs were captured, with a density of 12.7 eggs.1000m^{-3}. Furthermore, only 36% of stations produced Snapper eggs, which were dispersed throughout the whole region (Fig. 4-19 in Fowler et al. 2020).

In 2018 in GSV/IS, the number of stations sampled was quite low because of the impact of poor weather on the sampling regime. As such, a shorter overall distance and lower total volume of water were sampled compared to 2019 (Table 4.4). Nevertheless, a relatively high number of Snapper eggs were captured that produced the highest regional density of 114.5 eggs.1000m^{-3}. These were broadly distributed across 80.4% of the stations but were particularly abundant in the north between Black Point and Port Adelaide (Fig. 4-16 in Fowler et al. 2019). In 2019, more stations and a considerably greater geographic area were sampled than in 2018, producing a relatively high number of Snapper eggs. The density was 71.4 eggs.1000m^{-3}, which were distributed throughout the whole region (Fig. 4-19 in Fowler et al. 2020).

4.4 Discussion

4.4.1 Comparison of Snapper egg surveys

Several studies have described the characteristics and development of Snapper eggs (Cassie 1956, Steer et al. 2017). The descriptions and stages of development were summarised here, to provide a comprehensive description of the egg and the developing embryo. Historically, such information has been used to differentiate Snapper eggs in wild plankton samples (Fowler unpublished data, McGlennon 2003, Zeldis et al. 2005, Wakefield 2010, Jackson et al. 2012). A significant advancement made in South Australia in recent years was the development of ISH processing, i.e., the molecular biology technique for identifying Snapper eggs (Oxley et al. 2017, Steer et al. 2017). Despite the potential of this new approach for reducing ambiguity in egg identification, its application in batch processing large numbers of samples has proven challenging (Fowler et al. 2020). So, it is still important to retain the capacity to identify Snapper eggs from their morphological characteristics, accounting for the emphasis in this chapter on the morphological characteristics of Snapper eggs and their development.

At different times over the past three decades, Snapper egg surveys have been done in the gulf waters of South Australia (McGlennon 2003, Steer et al. 2017, Fowler et al. 2019, 2020). Throughout this considerable period, there have been some consistent aspects to the sampling as well as numerous modifications to the sampling methodology and regime. All surveys have been done from the MRV *Ngerin*. During the 1990s, 2000 and then in 2018 to 2020, oblique tows with double bongo nets were undertaken to sample the plankton throughout the water column. This is the methodology that has generally been used for Snapper plankton surveys done in other places including Western Australia (Wakefield 2010, Jackson et al. 2012), Port Phillip Bay (Hamer et al. 2011), and New Zealand (Zeldis et al. 2005). In South Australia, the primary variation away from this was in 2013, 2014 and 2015, when vertical net tows were done during the study that was aimed at developing appropriate techniques for undertaking DEPMs (Steer et al. 2017). It is now apparent that the vertical tows were too short and the volumes of water sampled were too low, which minimised the probability of catching Snapper eggs or larvae. So, the low catches of eggs during these years can be partly attributable to the low volumes of water sampled. In comparison, the double oblique tows that were done recently sampled approximately seven times the volume of water, which significantly increased the possibility of catching Snapper eggs.

In South Australia, despite the use of double oblique plankton tows in some surveys, the absolute numbers of Snapper eggs and their concentrations have generally been low compared to results from other studies. For example, during the 1980s, in the Hauraki Gulf in New Zealand, plankton surveys were done monthly during the reproductive season using double oblique bongo tows throughout three seasons (Table 4.5). Through these surveys the mean density of Snapper eggs ranged from 290 to 4,370 eggs.1000m^{-3}. As such, the lowest mean density in the Hauraki Gulf was more than twice the highest recorded in South Australia, and the density estimates were generally one or two orders of magnitude greater (compare density estimates in Tables 4.4 and 4.5).

Table 4.5. Estimates of density of Snapper eggs recorded from plankton surveys undertaken in the Hauraki Gulf during the 1980s (from Zeldis et al. 2005).

Region	Year (month)	Mean density (no.1000m^{-3})
Hauraki Gulf (NZ)	1985/86 Nov	1,900
	1985/86 Dec	1,470
	1985/86 Jan	560
	1986/87 Nov	2,680
	1986/87 Dec	4,660
	1986/87 Jan	290
	1987/88 Nov	4,370
	1987/88 Dec	2,820
	1987/88 Jan	490

From 1997 to 2007, annual ichthyoplankton surveys were undertaken for the Snapper stocks in Shark Bay, Western Australia, (Jackson et al. 2012). The sampling method was similar to that used in South Australia, but the absolute numbers of Snapper eggs captured in some surveys were often many times higher than the numbers captured in South Australia, even from fewer stations (Table 4.6). For example, in June 2000, a total of 22,801 Snapper eggs were sampled from 124 stations in the Eastern Gulf of Shark Bay. For the surveys done in South Australia, the highest estimate was 2,672 eggs from 38 stations, as recorded in December 1995. In 2020, there were 1,586 Snapper eggs from 265 stations sampled in GSV/IS (Table 4.4). Furthermore, in Shark Bay, the range in estimates of Snapper eggs captured per station was from 1.01 to 183.9 and often exceeded 100 eggs.station^{-1} (Table 4.6). In comparison, the range in catch rates in South Australia was much more limited, i.e. 0.14 to 12.5 Snapper eggs.station^{-1}, and were generally <10 eggs.station^{-1}, except for the exceptional catch rate of 70.32 eggs.station^{-1} in December 1995 (Table 4.4).

In Western Australia, Snapper egg surveys were also undertaken in Cockburn Sound during the reproductive seasons between 2001 to 2004 (Wakefield 2010). The summarised results are difficult to compare with those from South Australia, however, the contour maps presented by Wakefield (2010) indicated that concentrations of Snapper eggs reached as high as 8,000 eggs.1000m^{-3}. Whilst clearly the mean densities would be much lower, nevertheless, the results suggest relatively high numbers of Snapper eggs were captured at particular places throughout the sample area.

Table 4.6. Details of results from Snapper egg surveys undertaken in Shark Bay, Western Australia between 1998 and 2007.

Location	Year	Month	No. stations	% stations with Snapper eggs	No. Snapper eggs	Snapper eggs per station
Eastern Gulf	1998	June	110	41	2112	19.2
Eastern Gulf	1998	July	82	24	83	1.01
Eastern Gulf	1999	June	115	64	13,526	117.62
Eastern Gulf	2000	June	124	56	22,801	183.88
Eastern Gulf	2001	June	117	62	16,910	144.53
Eastern Gulf	2002	June	117	48	323	2.76
Eastern Gulf	2003	May	102	46	3,908	38.31
Eastern Gulf	2004	June	113	35	427	3.78
Denham Sound	1998	June	79	53	1,088	13.77
Denham Sound	1998	July	77	58	1,001	13
Denham Sound	1999	July	94	78	883	9.39
Denham Sound	2000	July	68	71	1,935	28.46
Denham Sound	2001	July	83	41	825	9.94
Denham Sound	2002	July	83	51	426	5.13
Denham Sound	2003	June	83	61	526	6.34
Freycinet	1998	Aug	91	49	16,643	182.89
Freycinet	1999	Sept	119	71	3,033	25.49
Freycinet	2000	Sept	95	73	12,698	133.66
Freycinet	2001	Aug	114	40	260	2.28
Freycinet	2002	Sept	116	64	2,847	24.54
Freycinet	2004	Sept	115	34	440	3.83
Freycinet	2006	Sept	116	50	866	7.47
Freycinet	2007	Sept	117	51	492	4.21

4.4.2 Conclusions

The purpose of this chapter was to synthesise information about plankton surveys that were done for Snapper eggs in South Australia's marine waters between 1994 and 2020 as part of applications of the DEPM to provide estimates of spawning biomass. This review has provided a comprehensive description of the characteristics and development of Snapper eggs. Furthermore, it is evident that over time the plankton sampling gear and tow types changed whilst total sample areas and the intensity of sampling gradually increased. Nevertheless, despite the increases in spatial area and sampling effort, the densities of the captured Snapper eggs have been consistently low compared with those from other Australasian places. It appears that, over time, the dispersion of Snapper eggs have become more dispersed, i.e., less concentrated in hotspots (Fig. 4.5). This might indicate that large spawning aggregations have become less significant.

It was the purpose of this review to inform rather than to provide critical assessment of the sampling methodology or intensity for the plankton surveys applied to the DEPM for Snapper. Such critical appraisal is complex and relevant questions have recently been considered by a Snapper DEPM Working Group at SARDI. The discussions of that group have contributed to the development of Theme 2 of the National Snapper Science Program that has been developed throughout 2023. Furthermore, an FRDC project to address the issues of improving the DEPM for Snapper has recently been funded. The empirical work for this project will be undertaken during the summers of 2023/24 and 2024/25.

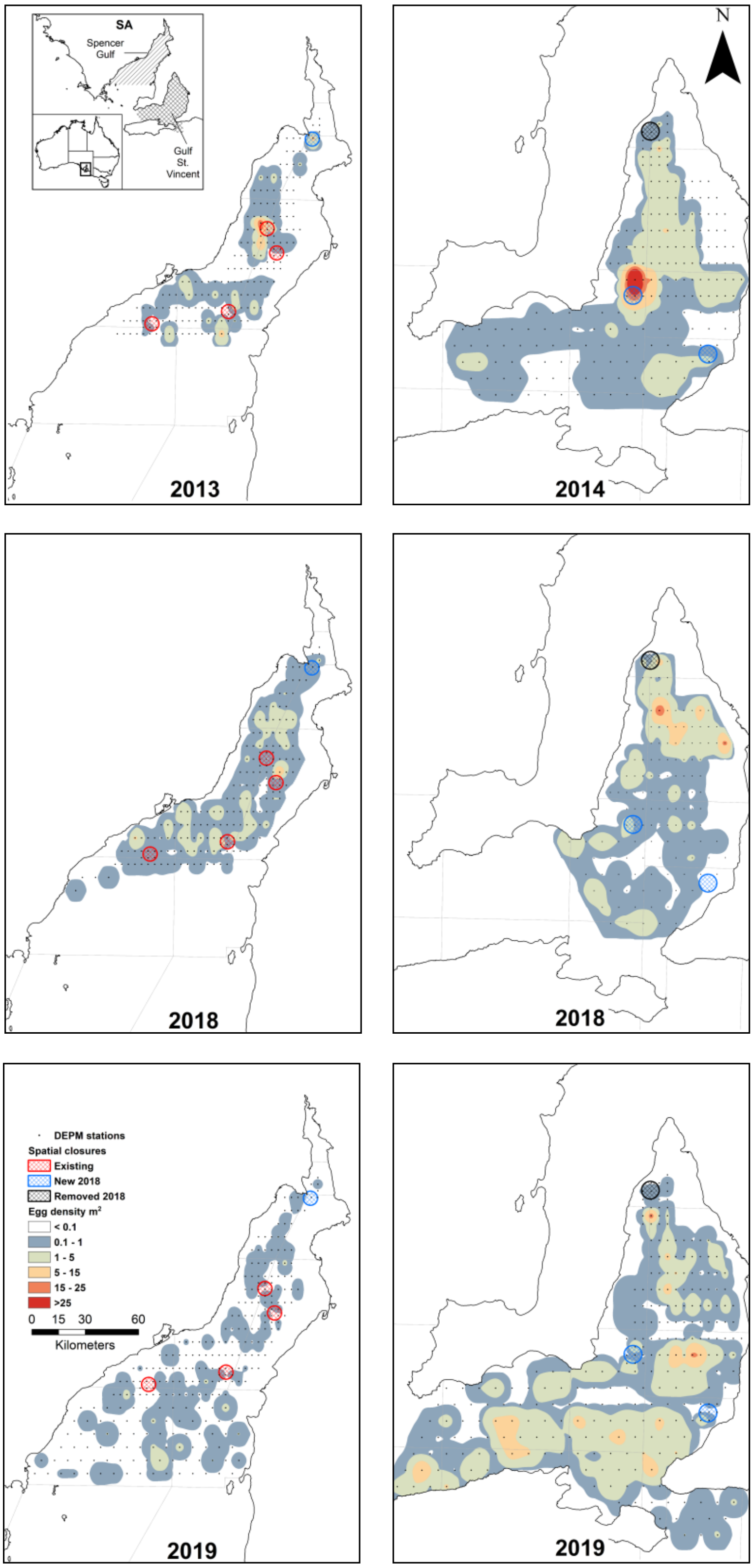


Fig. 4.5. Estimates of the densities of Snapper eggs in Spencer Gulf in 2013, 2018 and 2019 and in Gulf St. Vincent in 2014, 2018 and 2019. The samples stations in each region and year are indicated as dots.

4.5 References

Ahlstrom, E.H., Moser, H.G. (1980). Characters useful in identification of pelagic marine fish eggs. CalCOFI Report Vol XXI. Pp 121-131.

Cassie, R.M. (1956). Early development of the Snapper, *Chrysophrys auratus* Forster. Transactions of the Royal Society of New Zealand. Vol 83 (4): 705-713.

Crossland, J. (1980). The number of Snapper (Forster), in Hauraki Gulf, based on egg surveys in 1974-75 and 1975-76. Fisheries Research Bulletin No. 22, Fisheries Research Division, Ministry of Agriculture and Fisheries, New Zealand.

Drew, M.J., Rogers, T.A., McGarvey, R., Feenstra, J., Matthews, D., Matthews, J., Earl, J., Smart, J., Noell, C., and Fowler, A.J. (2022). Snapper (*Chrysophrys auratus*) Stock Assessment Report 2022. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2007/000523-7. SARDI Research Report Series No. 1155. 178 pp.

Fowler, A.J. (2002). Snapper (*Pagrus auratus*). South Australian Fisheries Assessment Series 2001/13. 64 pp

Fowler, A.J., Steer, M.A., McGarvey. R., Smart, J. (2019). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2019/000331-1. SARDI Research Report Series No. 1031. 62pp.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Jackson, G., Cheng, Y.W., Wakefield, C.B. (2012). An evaluation of the daily egg production method to estimate spawning biomass of Snapper (*Pagrus auratus*) in inner Shark Bay, Western Australia, following more than a decade of surveys 1997-2007. Fisheries Research 117-118: 22-34.

Lasker, R. (1985). An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*)). US Department of Commerce. NOAA Technical Report NMFS 36, 99 pp.

McGlennon, D. (2003). The fisheries biology and population dynamics of Snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. PhD Thesis, University of Adelaide, Adelaide, South Australia. 212pp.

Oxley, A.P.A., Catalano, S.R., Wos-Oxley, M.L., Westlake, E., Grammer, G., Steer, M.A. (2017). Using in situ hybridization (ISH) to extend the Daily Egg Production Method (DEPM) to new species. Molecular Ecology Resources 17: 1108-1121.

Steer, M.A., McGarvey, R., Oxley, A., Fowler, A.J., Grammer, G., Ward, T.M., Westlake, E., Matthews, D., Matthews, J. Developing a fishery independent estimate of biomass for Snapper (*Chrysophrys auratus*). Final report to FRDC (Project No. 2014/019). 68pp.

Wakefield, C.B. (2010). Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. Journal of Fish Biology 77: 1359-1378.

Zeldis, J.R. (1993). Applicability of egg surveys for spawning stock biomass estimation of Snapper, Orange Roughy, and Hoki in New Zealand. Bulletin of Marine Science 53: 864-890.

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

Zeldis, J.R., Oldman, J., Ballara, S.L., Richards, L.A. (2005). Physical fluxes, pelagic ecosystem structure and larval fish survival in Hauraki Gulf, New Zealand. Canadian Journal of Fisheries and Aquatic Sciences 62: 593-610.

4.6 Appendices

4.6.1 Appendix 4.1 – General development of marine fish eggs

Here is a general description of some processes involved in fish egg development based on descriptions provided in Lagler et al. (1977). It introduces some terminology and describes some processes and visual changes that occur during egg development. At fertilisation, the **sperm** enters the egg through the **chorion** via the **micropyle**, allowing the nucleus of the egg cell and the sperm to make union in the cytoplasm of the egg. When the egg is fertilised, the cytoplasm that is distributed amongst the yolk separates from the yolk and forms the germinal disc or **blastodisc**, at the animal end of the egg. Subsequently, the blastodisc undergoes **cleavage**, i.e. the division of the blastodisc into successively smaller cells called blastomeres, which are spread out as a flat plate on the upper surface of the yolk mass. For most fish species, cleavage is **meroblastic**, i.e., is restricted to the cells of the blastodisc, whilst the yolk does not divide.

Cleavage results in the formation of two kinds of cells, the **blastoderm** and the **periblast**. The blastoderm cells produce the embryo. The periblast cells lie between the cells of the blastoderm and cover the entire yolk mass. The under-rim of the blastodisc thickens to form the '**randwulst**' or marginal ridge which comes to have an inner layer, i.e., the **germ ring**. Caudally, the ring is thickest and is recognised as the embryonic shield.

The **hypoblast** is an involuted cell mass that is formed during gastrulation. The presumptive endodermal cells at the caudal edge of the embryonic shield turn inward beneath the blastoderm and then stream forward beneath it, becoming the endodermal portion of the hypoblast. For this incursion of cells, an opening, i.e., the **blastopore** appears at the tail end of the embryonic shield. Also, moving inward over the dorsal lip of the blastopore are cells of the prechordal plate and notochord that establish the embryonic axis. Presumptive mesodermal cells also migrate inward over the lip of the blastopore and position themselves on both sides of the embryonic axis beneath the ectoderm. The endodermal and mesodermal components of the hypoblast become organised to establish the primordia of the internal organ systems.

Epiboly is the cellular overgrowth of the yolk that occurs whilst the embolic processes of involution of cells occurs. 'Randwulst' and germ ring cells not involved in involution accompanied by presumptive ectodermal cells, grow to cover the yolk mass outwardly as **epiblast**. The periblast provides, through growth, an inner covering of the yolk mass. The initial periblast cells and epiblast, in covering the yolk, form the yolk sac. As epiboly is proceeding, the presumptive neural plate, forerunner of the central nervous system transforms into a ridge-like keel along the mid-dorsal line. This solid keel, in contact with notochordal cells beneath, gradually becomes overgrown by epidermis and eventually becomes tubulated to form the hollow neural tube.

5. LARVAL DEVELOPMENT AND CAPABILITY, DISTRIBUTION AND ABUNDANCE

Anthony Fowler and Troy Rogers

5.1 Introduction

The population dynamics and fishable biomass of Snapper in South Australia are fundamentally driven by high inter-annual variation in recruitment, i.e., the numbers of 0+ juveniles that recruit to populations (Fowler and Jennings 2003, Fowler and McGlennon 2011). Different trends in recruitment throughout the 2000s, have meant that the two main South Australian Snapper stocks have experienced different trends in fishable biomass and fishery catches (Fowler et al. 2020). Given this, at the recent National Snapper Science and Management Workshop (FRDC 2019/085), it was acknowledged that the management of these fisheries would benefit from developing some understanding of the causes of variable recruitment (Cartwright et al. 2020). Previous work on Snapper populations in Victoria and New Zealand has demonstrated that recruitment year class strength is established very early in the life history, reflecting inter-annual variation in the survivorship of recently hatched larvae (Zeldis 2005, Murphy 2012, 2013). To understand the dynamics in the South Australian Snapper stocks, it could be beneficial to consider their early life history, i.e., the distribution, abundance, and spatial connectivity throughout the planktonic stages.

It is apparent from work done throughout the 2000s that larval fish can have considerable swimming capacity that is sufficient to influence their dispersal, based on the interaction between their behaviour and the influence of water movement associated with ocean currents (Leis 2010, Leis et al. 2011). Furthermore, it is possible to simulate such dispersion using biophysical models which integrate biological information with physical oceanographic models. The use of such biophysical models to consider larval fish movement depends on understanding the changes in the capabilities of the larvae throughout their ontogenetic development with respect to; swimming, orientation, vertical distribution, and their sensory capabilities with respect to vision, hearing and olfaction (Clark et al. 2005; Leis et al. 2006; Leis 2007, 2020).

The aim of this chapter was to describe the ecology of the larval life history stage for South Australian Snapper. To achieve this, the specific objectives addressed were:

1. to describe the ontogenetic development of Snapper larvae to assist in identifying them in plankton samples;
2. to describe growth and the increase in capacity as the larvae develop;
3. and to describe the patterns of distribution and abundance of Snapper larvae from plankton samples collected from Spencer Gulf, Gulf St. Vincent (GSV) and Investigator Strait (IS). Such data are important when considering how the larvae disperse.

5.2 Materials and methods

5.2.1 Larval development series

Adult Snapper were captured in the summer of 2019/20 and maintained as brood stock at SAASC throughout 2020. The adults were spawned in batches during late 2020 to provide juvenile fish for a stock enhancement project. Through the summer of 2020/21, the larvae were reared throughout their development. On a regular basis, a small number of developing larvae were removed from rearing tanks, examined, and then photographed using an image analysis system. This allowed the morphological development of the larvae to be documented in relation to their size and age.

5.2.2 Ontogenetic development and capacity for dispersion

A desk-top study was undertaken to assimilate data and information about the early life history of Snapper from different sources. This involved information on the growth, development and swimming capabilities of Snapper larvae from studies that have been done in Australia, New Zealand and elsewhere. This included early life history information from a recruitment study done between 2000 and 2010 in Northern Spencer Gulf (NSG) (Fowler and Jennings 2003, Fowler et al. 2010). That study involved an annual demersal trawl survey that provided specimens of 0+ fish (Fig. 5.1), for which the early life history was described through the retrospective analysis of the microstructure of their otoliths (Chapter 8, Fowler and Jennings 2003, Saunders 2009, Fowler et al. 2010). Sagittae from juvenile Snapper display a microstructure that informs about fish age and the timing of events that occur during their ontogenetic development (Appendix Fig. A5.1). These otoliths show a settlement mark that corresponds to the timing of settlement from the planktonic to the benthic environment, allowing differentiation between the pre- and post-settlement life history stages (Fowler and Jennings 2003). Furthermore, for juvenile Snapper there is a linear relationship between otolith size and fish size, which allows the somatic growth pattern to be back-calculated from the widths of daily otolith growth increments. Throughout the 2000s, the microstructure of otoliths from wild juvenile Snapper captured in NSG were used to provide comprehensive analyses of growth and the timing of life history events (Fowler and Jennings 2003, Saunders 2009, Fowler et al. 2010). Also, for several juvenile fish collected in each of 2000, 2001 and 2002, a trajectory of increment widths was measured from the otolith core to its outside margin (Fowler and Jennings 2003). These trajectories of increment widths were used to calculate daily somatic growth increments using the biological intercept method to estimate size-at-age (Campana 1990, Campana and Jones 1992). Then, average growth curves were developed for each year. For this chapter, because the focus is on the pre-settlement phase of the life history, growth through the first 30 days was considered, to cover the larval period, settlement, and a few days post-settlement.

Fig. 5.1. Photograph of juvenile Snapper captured by otter trawling in NSG during one of the annual recruitment surveys undertaken between 2000 and 2010 (Fowler et al. 2010).

5.2.3 Distribution and abundance of Snapper larvae

A number of plankton sampling programs have been undertaken in NSG since the 1990s and in Gulf St. Vincent and Investigator Strait between 2013 and 2020. The details regarding sampling methodologies, protocols and the catches of Snapper eggs were summarised in Chapter 4. The plankton samples collected during each field trip were processed in several stages. During the first stage of processing, the fish eggs and larvae were removed from each plankton sample into separate vials. Later, the samples of fish eggs were examined, and any Snapper eggs were identified based on morphological characteristics and/or ISH processing (Chapter 4). Then, between July and December 2020, the fish larvae from the samples were examined to identify the Snapper, based on the larval development series from the reared fish (Appendix 5.6.2), and published descriptions (Neira et al. 1998). The data were compiled for each year and interpreted as region-specific patterns of distribution and abundance of the larvae.

5.3 Results

5.3.1 Snapper larval characteristics and development

The descriptions of post-hatch Snapper larvae and their development (Appendix A5.6.2), are based on descriptions and morphological characteristics provided by Cassie et al. (1956) and Neira et al. (1998). The former considered larvae that were reared from adult brood stock in New Zealand, which were considered for the few days until the metabolism of the oil globule and yolk sac was completed. For the descriptions of later stage larvae that were provided by Neira et al. (1998), there were only 26 specimens available that were in the size range of 3.0 – 13.3 mm BL, most from New South Wales and one from Western Australia. Consequently, the larvae considered in the published descriptions (Cassie 1956, Neira et al. 1998), were from stocks other than those in South Australia (Chapter 10). Given the genetic differences between the Australasian stocks, it is possible that the larvae collected in South Australia may have some morphological differences from the published descriptions. Since the photos of larvae presented in Appendix A5.6.2 were reared at SAASC from brood stock captured locally, they provide the best reference material to assess the fish larvae from wild plankton samples collected in South Australia.

5.3.2 Events and phases of ontogenetic development

A model that describes the ontogenetic development of Snapper larvae is presented in Fig. 5.2. Six important events divide the early life history into different ontogenetic phases. Understanding of these stages and phases is described below, followed by a description of growth throughout the pre-settlement duration, and collation of information on the development of swimming capacity. The focus of the descriptions is on the relative timing of the different events and duration of the phases throughout the pre-settlement development. The developing capabilities ultimately determine the extent to which the larvae can influence their own dispersal throughout the phases of ontogenetic development. Such information is used when developing biophysical models that describe the process of larval dispersal throughout the period of their development.

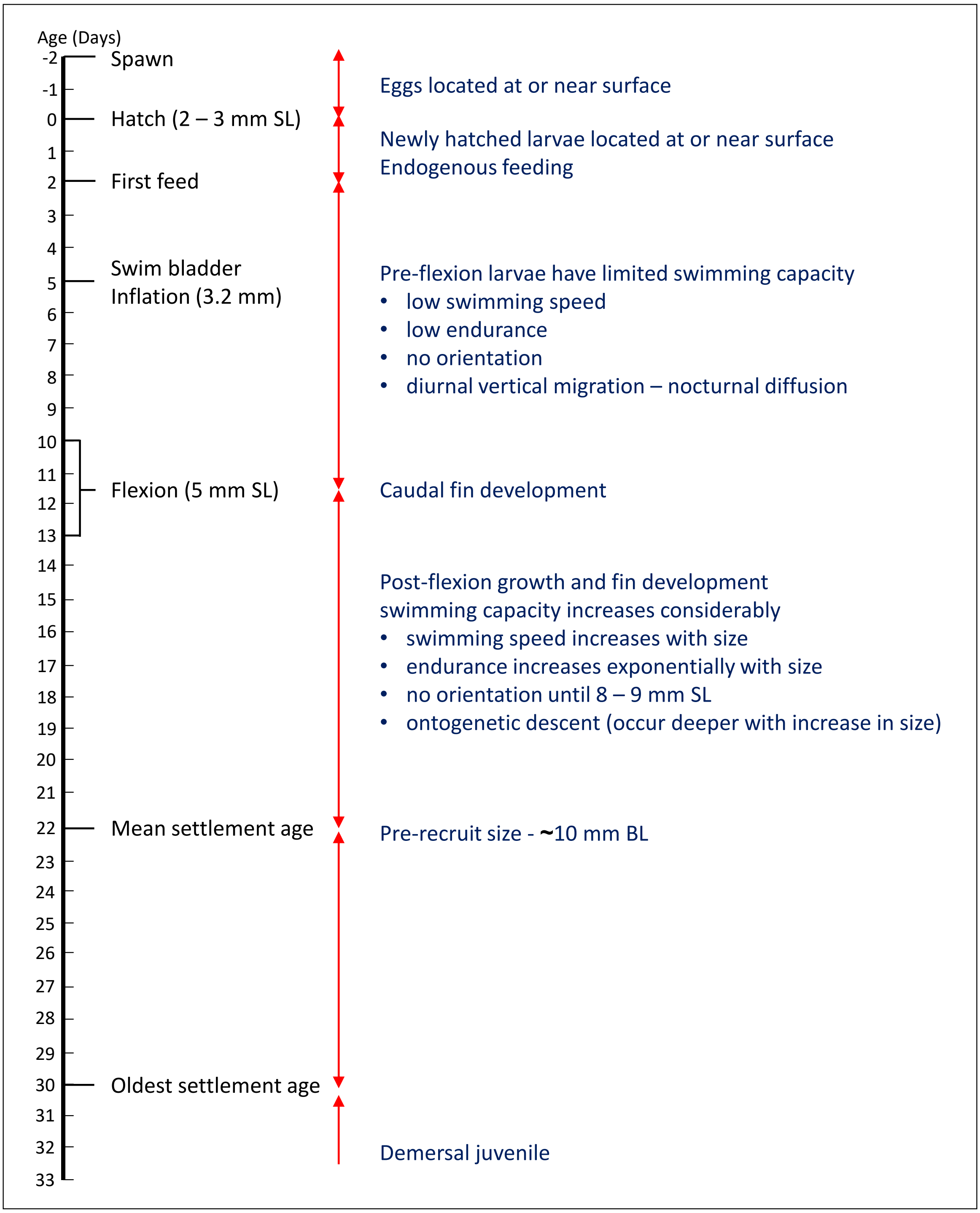


Fig. 5.2. Conceptual model showing the stages of development of Snapper larvae. These are related to larval age from hatch in days and to fish size and swimming capabilities.

Spawning

Ultimately, to consider Snapper larval ecology and potential dispersion throughout their development, it is beneficial to know where and when the eggs are introduced into the ecosystem. For this, our understanding of spawning in South Australian waters varies at different temporal scales. Reproduction occurs during the warmer months (Chapters 2, 3). However, at smaller temporal scales, there is poor understanding about the timing and periodicity of spawning. It is uncertain whether there is lunar periodicity to spawning, as occurs in Cockburn Sound, Western Australia (Wakefield 2010). There is also uncertainty about the diurnal periodicity of spawning. For plankton samples from NSG during the 1990s, the time of day when Snapper spawned was estimated by subtracting the ages of eggs based on their stage of development and SST, from the times of day when captured (McGlennon 2003). The resulting estimates suggested that spawning most commonly occurred from 14:00 to 24:00 hours, with the median spawn times from 17.3 to 18.7 hours in the late afternoon and early evening. This is consistent with results from 2000, which suggested spawning occurred during the early evening (Fowler pers. obs). Alternatively, for Snapper in New Zealand, Crossland (1980) concluded that spawning began 3-4 hours after dawn, peaked in the early afternoon and continued until dusk, which meant that most eggs were spawned between 08:00 and 20:00, with a tendency towards earlier in the day as the season progressed.

The main features and characteristics of the Snapper eggs were described in Chapter 4. They include: a single, large oil globule that occupies the upper pole of the sphere, which makes the eggs positively buoyant, i.e., they float to the surface in still water (Cassie 1956). Consequently, subject to weather and sea conditions, it is expected that Snapper eggs would occur in the upper part of the water column, if not at the surface.

Hatching

Experimental trials that considered the development times of Snapper eggs indicated that there is a strong influence of water temperature, but minimal influence of salinity (McGlennon 2003). In the latter study, the approximate elapsed times between when eggs were placed in experimental treatments until 50% had hatched varied considerably, and demonstrated a negative relationship with water temperature, as indicated below (note that these times are likely to under-estimate the actual development times between fertilisation and hatch since they relate to the times from when the eggs were placed in the experimental containers):

- 18°C – (31.75 – 33.75 hrs);
- 21°C – (22.75 – 26.0 hrs);
- 24°C – (17.25 – 19.0 hrs).

At hatch, Snapper larvae are relatively undeveloped and small. They are positively buoyant and are held inverted at the surface, with the yolk and oil droplet located upwards and the head displaced laterally (Pankhurst et al. 1991). Estimates of size-at-hatch are quite consistent and include: the range of 2.1 – 3.1 mm BL (Neira et al. 1998); 2.06 mm SL (Pankhurst et al. 1991); 2.6 mm TL (Fowler and Jennings 2003); 2.2 – 2.6 mm BL (Appendix A5.6.2).

Seasonal SST regimes vary regionally in South Australian waters (Chapter 3). Furthermore, within certain regions there is inter-annual variation in SSTs. Such spatial and temporal variation in SST would likely influence the period of egg development. Several studies have considered the water temperatures for NSG throughout the Snapper spawning season. For the summers of 1999/00, 2000/01, and 2001/02, data were accessed from satellite imagery (Fowler and Jennings 2003), whilst electronic loggers were used to record water temperature through the summers of 2005/06, 2006/07 and 2007/08 (Saunders 2009, Saunders et al. 2012). Whilst there was considerable inter-annual variation in water temperature regimes, the studies demonstrated consistent differences between the important spawning months of December and January. During December, mean water temperature generally increased from approximately 20 – 22 °C, whilst during January the water temperatures tended to stabilise around 23 - 24°C. From this, it is expected that egg development would be more rapid during January.

First feed

During the first one or two days immediately after hatching, Snapper larvae endogenously metabolised the yolk and oil globule (Pankhurst et al. 1991). They also righted themselves so that the dorsal surface was facing upwards. Through this time, the larvae became negatively buoyant and predominantly held a ‘resting posture’, whereby they sank slowly with the head down and the body held at an angle of 45° to the water surface (Pankhurst et al. 1991). Undulations of the body and tail produced an eccentric spiral swimming motion that periodically returned the larvae to the surface. They also displayed a ‘startle response’.

For larvae reared at SAASC during the early 2000s, the period of endogenous feeding lasted for two days as the larvae first consumed extraneous food on the third day. The period of transition from endogenous to exogenous nutrition was characterised by a retarded increase in length that coincided with: depletion of yolk and oil droplet reserves; mouth opening; eye pigmentation; and swim bladder inflation (Pankhurst et al. 1991). For reared larvae, this corresponded with formation of the first daily increment in the sagittae at a mean radius of 3.32 μm from the primordium (Fowler and Jennings 2003), whilst for wild-caught Snapper larvae the first increment was evident at 3.53 μm from the primordium. From the time of hatching onwards, the larvae maintained a horizontal swimming position (Pankhurst et al. 1991). During the ‘photophase’, young larvae searched for and attacked prey, whilst at night they returned to the ‘resting posture’.

Swim bladder inflation

As with other fish species, Snapper larvae initiate inflation of the swim bladder at night by ‘gulping’ air from the surface, which passes through the pneumatic duct into the swim bladder (Partridge et al. 2003). For reared Snapper larvae, initial swim bladder inflation occurred 4 – 5 days after hatch at a mean size of 3.17 mm SL (Pankhurst et al. 1991). This night-time inflation by the larvae may act as a buoyancy regulator allowing them to maintain position in the water column with minimum effort, and to rest and conserve energy when it is too dark to feed (Hunter and Sanchez 1976, Hoss et al. 1989). The growth rates of Snapper larvae with inflated swim bladders have been higher than those for which it had not occurred successfully (Battaglene and Talbot 1992).

Flexion

A notable process during larval development is ‘notochord flexion’, i.e., the bending upward of the notochord tip associated with caudal fin formation. After transition from endogenous to exogenous feeding and swim bladder inflation, the Snapper larvae showed a period of accelerated growth that continued until flexion. Estimates of the timing of notochord flexion for Snapper larvae from different studies are quite consistent: at approximately 5 mm SL and 18 to 24 days (Pankhurst et al. 1991); at 5 – 6 mm SL at about 16 – 18 days after hatching (Clark et al. 2005); and for wild-caught larvae at 5.0 – 6.6 mm BL (Neira et al. 1998). For the development series based on larvae reared in South Australia, flexion was apparent from Day 17 (Appendix 5.6.2, Fig. A5.8).

Settlement

Between flexion and settlement, the larvae grew, developed, and formed the fins. Comprehensive information on pre-settlement duration is available for Snapper juveniles collected from NSG (Chapter 8, Fowler and Jennings 2003, Saunders 2009). The estimates range from 15 to 30 days, with the mean of 22 days. Estimates of size-at-settlement were calculated in 2000, 2001 and 2002, and ranged from 7.2 to 13.7 mm CFL, with the mean generally around 10 mm CFL. The estimates of both parameters were considerably lower than provided in the literature. Neira et al. (1998) indicated that settlement occurred at ~12.0 – 13.3 mm BL, whilst Clark et al. (2005) suggested that settlement occurred at approximately 30 days post hatch when the larvae were ~10.0 mm SL.

5.3.3 Analysis of growth throughout the larval ontogeny

Growth through the larval stage for Snapper has been monitored and described for reared fish in New Zealand (Pankhurst et al. 1991). The larvae sampled regularly from rearing tanks and measured for SL, showed three phases of growth:

1. the first phase occurred between hatching and first feeding, corresponding to the period of endogenous nutrition. It lasted approximately three days and was characterised by an initial rapid increase in length prior to mouth opening and first-feeding;
2. there was an intermediate phase of growth associated with transition from endogenous to exogenous nutrition that occurred through ages 3 – 6 days post-hatch. This was a period of slow growth that coincided with: depletion of yolk and oil droplet reserves; mouth-opening; eye pigmentation; and swim bladder inflation;
3. the third phase was associated with an extended period of accelerating growth that occurred from approximately the age of eight days onwards for reared larvae (Pankhurst et al. 1991), during which growth was based entirely on exogenous feeding as the larvae captured their prey. Growth rates through this period increased exponentially until near settlement.

Growth of Snapper larvae was also described retrospectively for wild-caught juveniles from trawl surveys in 2000, 2001 and 2002 in NSG (Chapter 8, Fowler and Jennings 2003). Their growth through the larval ontogeny was described from back-calculation of somatic growth rates from the widths of daily increments in the otoliths (Fig. 5.3).

For 2000 and 2001, the fish that were considered included some that had settled both earlier and later in the season. Generally, two phases of growth were evident (Fig. 5.3). During the first eight to 10 days post-hatch, the growth rates were very low at 0.2 – 0.4 mm.day^{-1}. For this early part of the ontogeny, the growth curves were essentially linear until the fish reached approximately 5 mm CFL. Subsequently, the growth rates increased exponentially. For the early recruits in 2000, the growth rates increased to ~0.9 mm.day^{-1}, whilst for those that settled later, the increase was slower to a lower maximum growth rate. At around 22 days post-hatch, the growth rates slowed down, presumably related to the settlement of the fish. Such growth rates produced logistic growth curves, with the early settlers reaching larger sizes-at-age compared with the later arrivals (Fig. 5.3). In 2001, the early and late settlers had marginally higher growth rates than in 2000, which resulted in larger sizes-at-age. Alternatively, in 2002, growth rates were lower than in 2000 and 2001, with the maximum growth rate of 0.8 mm.day^{-1}. As such, the growth curve was flatter with the fish reaching only 15 mm CFL by 30 days of age.

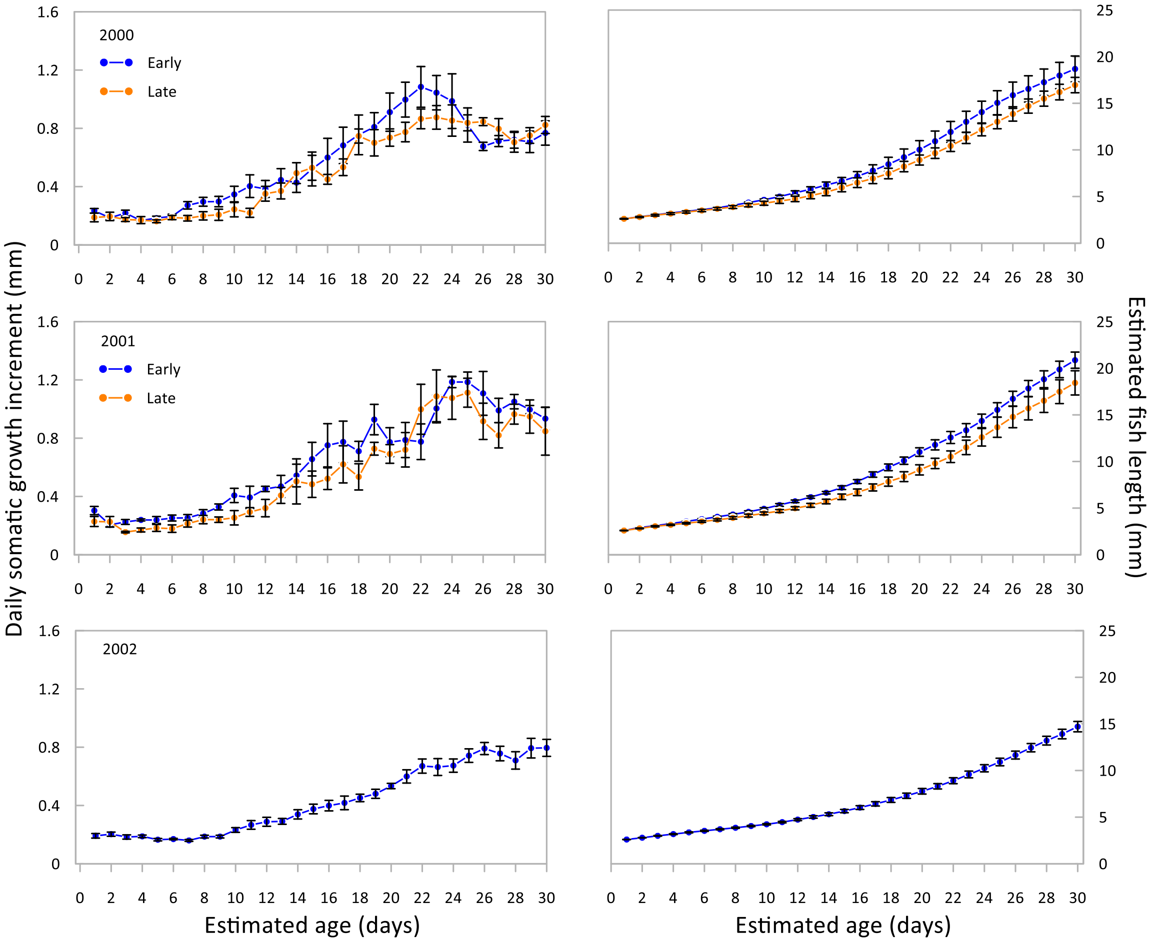


Fig. 5.3. Trajectories of estimates of average (+SE) somatic growth rate (left) and estimated growth curve (right) derived by back-calculation from measurements of daily micro-increments in otoliths for juvenile fish sampled in 2000, 2001 and 2002. Figures for 2000 and 2001 compare the trajectories for early and late settlers, each based on sample sizes of five fish. For 2002, all eight juvenile fish captured were included.

5.3.4 Analysis of swimming capabilities throughout larval ontogeny

Review of literature on swimming capabilities

Some information on the swimming capabilities of Snapper larvae is available from empirical studies done both in the lab (Clark et al. 2005) and in the field (Leis et al. 2006). In the former study, two parameters, i.e., U_{crit} and 'endurance' were assessed using a multi-lane swimming chamber. U_{crit} or 'critical speed' is a laboratory raceway measure of potential swimming ability, whereby the speed of the current is increased incrementally in short steps until the larva can no longer swim against it. For Snapper, there was an exponential increase in U_{crit} with larval size that was described by the 'flat' curvilinear model [$U_{crit} = 0.47e^{0.41SL}$], although there was considerable variation in swimming speed with size. The fastest larvae were in the size range of 7.2 to 10.4 mm SL, which swam at 16.6 to 27.3 cm.sec^{-1}, i.e. from 1 to 5 cm.sec^{-1} faster than the average larvae. U_{crit} increased at a greater rate per unit growth following flexion, and such post-flexion larvae had mean critical speeds that were three to four times faster than those of pre-flexion larvae. As a generalisation, Snapper larvae at the times of flexion and then settlement could swim at mean critical speeds of around 5 cm.sec^{-1} and 10 – 20 cm.sec^{-1}, respectively. When U_{crit} was scaled to body length the scaled speed (body lengths.sec^{-1}), increased at about 2.5 – 2.8 body length.sec^{-1} for each increase in body length of 1 mm, to a maximum of 20 body lengths.sec^{-1}.

The relationships between 'endurance' and size for Snapper larvae is best described by an exponential or power model, [endurance = $0.0043e^{0.79SL}$]. This relationship is characterised by very low estimates of endurance for pre-flexion larvae (4 – 133 m), which improved at an increasing rate once flexion was complete, with a notable increase for those of about 6 – 7 mm SL (Clark et al. 2005). The increase in endurance that occurred following flexion was concomitant with formation of the caudal fin. The mean endurance for larvae of 4 – 5 mm SL was 250 m, which increased to 3 - 4 km for larvae of 6 - 7 mm SL and to 5 – 10 km for larvae of 9 – 10 mm SL (Clark et al. 2005). Average settlement-sized larvae would be capable of swimming at least 12 km at 10 cm.sec^{-1} without food or rest, and probably three times that distance if they fed, whilst the best performers could do much better. By settlement, a mean endurance of 10 km or more was possible over several consecutive days.

In the field, the swimming capabilities of Snapper larvae were also considered. Lab-reared larvae were released in open water environments and then followed by a diver who recorded data for '*in situ*' swimming speed, orientation, and vertical distribution (Leis et al. 2006). This was achieved for 23 post-flexion larvae that ranged in size from 7.0 to 9.3 mm SL. For the linear relationship between fish size and swimming speed ['*in situ*' swimming speed = 2.01(SL) – 10.6], there was a maximum speed of 12 cm.sec^{-1}, although with considerable variation amongst individuals. There was also a weak relationship between fish size and scaled swimming speed [swimming speed = 1.65(SL) – 6.48], giving scaled body speeds of 7 body lengths.sec^{-1} at 8 mm SL and 10 body lengths.sec^{-1} at 10 mm SL. The larvae fed '*in situ*' with little or no alteration in speed or direction, suggesting the likelihood that '*in situ*' swimming speeds could be sustained over long periods and distances. When considered across a number of species, there is a strong correlation between '*in situ*' measures of swimming speed and estimates of U_{crit} measured in the lab with estimates of U_{crit}, on average, 2.5 times that of the '*in situ*' measure.

The smallest Snapper larvae showed no significant orientation during swimming, but those that were 8-9 mm SL did show oriented swimming. Furthermore, the larger larvae also moved deeper in the water column as they increased in size, i.e., larvae occurred deeper in the water column as they got older. There was an ontogenetic descent in post-flexion larvae, and those of 10 – 15 mm SL swam near the bottom in the estuary of Lake Macquarie, NSW (Trnski 2002).

Consideration of factors for developing a biophysical model for the dispersal of Snapper larvae

The different phases and stages through the ontogenetic development of Snapper during their early life history are summarised in Fig. 5.2. Snapper eggs are positively buoyant because of the presence of a large single oil globule (Chapter 4). Their development is temperature-dependent and takes a day or two (McGlennon 2003). At hatch, the small, undeveloped larvae remain near the surface because of the buoyancy associated with the oil globule. After approximately two days, during which the larvae metabolise the yolk, the larvae begin exogenous feeding.

During the pre-flexion phase, i.e., a period of approximately 10 days between first feed and flexion the larvae are small and have no developed fins (Fig. 5.2, Appendix 5.6.2, Figs. A5.2, A5.3, A5.4). As such, they have limited swimming capacity and endurance. Through this period, they undergo swim bladder inflation. Like other species of finfish, Snapper larvae inflate their swim bladder during the night (Partridge et al. 2003), which is thought to allow them to hold station at night by slowing down their rate of sinking leading to conservation of energy. In Port Phillip Bay, the pre-flexion Snapper larvae displayed nocturnal diffusion diurnal vertical migration (DVM) (Murphy et al. 2011). At night, the pre-flexion larvae were distributed broadly throughout the water column. Alternatively, during the day, they aggregated in a mid-water depth zone at around 4 m. This appeared to optimise the foraging conditions, as the larvae at this depth zone had higher feeding success, relating to the distribution of the prey. Night-time sampling off Sydney, eastern Australia, also showed Snapper larvae to be distributed throughout the water column from near the surface to approximately 60 m in depth (Smith 2003). The distribution of Snapper larvae in mid-water during the day was also apparent in the Hauraki Gulf, New Zealand, although at night they were more abundant near the seabed, rather than being diffused throughout the water column (Parsons et al. 2014).

Flexion for Snapper larvae occurs at ~5.0 mm SL when they can swim at around 5 $cm.sec^{-1}$. After flexion and up to settlement, the larvae develop their fins and double their length. Their swimming speed increases linearly with size according to the relationship ['in situ' swimming speed = 2.01(SL) – 10.60]. During the early post-flexion period, swimming directionality remained random (Leis et al. 2006). However, once the larvae reached 8 - 9 mm SL in size, their 'in situ' swimming demonstrated directionality. Also, between the sizes of 7.0 to 9.3 mm SL, the larvae demonstrated ontogenetic descent, i.e., they occurred deeper in the water column, at least during the day when it was possible for divers to actively follow the swimming larvae (Leis et al. 2006). It remains uncertain whether this would have occurred at night or whether behaviour around DVM would have continued. Ultimately, the settlement-stage larvae swam close to the sea bottom (Trnski 2002), and when they experienced the appropriate habitat underwent settlement, oriented to the current and held position. A summary of the relationship between the pre-settlement development stages, swimming capacity and position in the water column is presented in Table 5.1.

Table 5.1. Stages of Snapper egg and larval development showing the characteristics significant for development of a biophysical model for dispersal throughout the early life history.

Stage	Size (mm)	Age (days)	Growth ($mm.day^{-1}$)	Duration (days)	Behaviour	Location
Spawning - egg	0.8 – 0.9	0	-	1 - 2	Buoyant, passive	Near Surface
Hatchling (hatch to first feed)	2.1 – 3.0	0 - 2	0.25	2	Buoyant, passive	Near surface
Pre-flexion (first feed to flexion)	2.6 – 5.0	2 - 12	0.3	10	DVM (nocturnal diffusion), poor swimmers, random orientation	Day – mid-water; night – distributed through water column
Post-flexion (Flexion to settlement)	5.0 - 10	12 - 22	0.52	10	DVM (nocturnal diffusion) Capable swimmers, late-stage show orientation	Day – occur deeper in water column; night – distributed throughout water column; prior to settlement located near bottom
Settlement	10	Mean = 22 (range 15–30)	-	-		Associated with bottom

5.3.5 Distribution and abundance of Snapper larvae

The numbers of Snapper larvae in the plankton samples from Spencer Gulf, Gulf St. Vincent and Investigator Strait were extremely low (Table 5.2). In 2000, the 75 stations that were sampled in NSG produced 941 Snapper eggs, but no Snapper larvae. Furthermore, across the four sampling programs undertaken in NSG between 2013 and 2019, a total of 28,364 fish larvae were captured that included only one Snapper larva. This one was 3.8 mm BL, was captured in December 2019 at Station 61 located northwest of Port Broughton adjacent to the Illusion.

Between 2014 and 2020, the number of fish larvae captured in Gulf St. Vincent and Investigator Strait during four surveys was 39,054 (Table 5.2). These included 83 Snapper larvae. In 2015, the one Snapper larva was 5.3 mm BL and was taken at Station 181, located in the middle of Investigator Strait north of Emu Bay. In 2018, two larvae were captured; one was 5.6 mm BL taken on the western side of the gulf southeast of Port Julia, the second was 5.0 mm BL captured off the Fleurieu Peninsula. In 2020, there were 80 Snapper larvae captured that were predominantly located in two areas (Fig. 5.4). The first was located on the eastern side of Gulf St. Vincent, offshore from the Adelaide metropolitan coastline north of Marino, which also produced the highest numbers of Snapper eggs in that year. The second area was throughout the western end of Investigator Strait, proximal to another area of relatively high numbers of Snapper eggs.

Table 5.2. Details of the total numbers of fish eggs and Snapper eggs, and fish larvae and Snapper larvae that were taken during DEPM surveys in Spencer Gulf and Gulf St. Vincent / Investigator Strait between 2013 and 2020.

Region	Year	Total fish eggs	No. Snapper eggs	Total fish larvae	No. Snapper larvae
NSG	2000	?	941	?	0
NSG	2013	31,909	81	6,261	0
NSG	2015	18,911	30	3,462	0
NSG	2018	69,668	1,204	7,967	0
NSG	2019	164,822	223	10,674	1
GSV/IS	2014	12,425	73	1,751	0
GSV/IS	2015	15,340	36	15,340	1
GSV/IS	2018	31,703	1,222	2,804	2
GSV/IS	2020	115,449	1,586	33,068	80

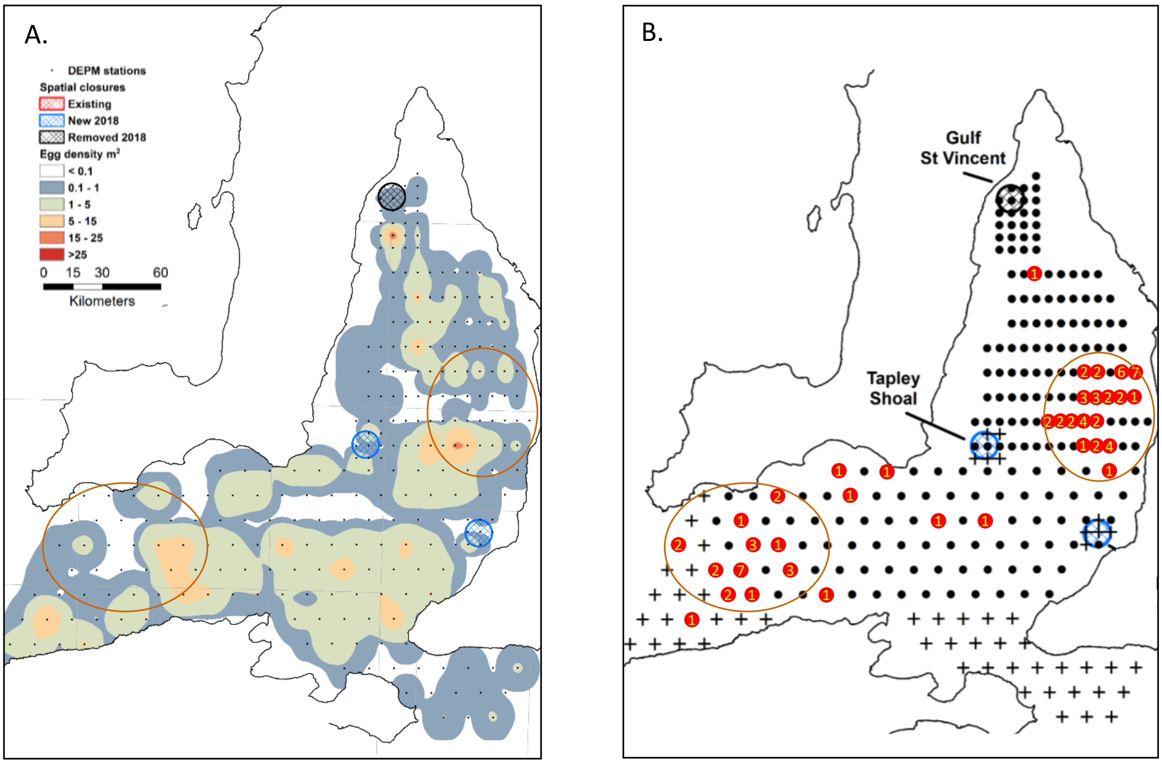


Fig. 5.4. Maps showing the distribution and abundance of Snapper eggs and larvae throughout Gulf St. Vincent and Investigator Strait, based on plankton sampling in January 2020. A. Estimates of the densities of Snapper eggs. B. Numbers of Snapper larvae sampled at the different stations. For both maps, the sample stations are indicated by black dots or crosses. The brown ovals on both maps indicate the two areas where the highest numbers of Snapper larvae were captured.

5.4 Discussion

5.4.1 Snapper larval characteristics and ontogenetic development

For the Snapper populations of southern Australia, recruitment is highly variable from year-to-year (Fowler and Jennings 2003, Fowler and McGlennon 2011, Hamer and Jenkins 2004), with year class strength established very early in the life history (Murphy et al. 2012, Murphy et al. 2013). As processes that occur during the early life history drive the population dynamics and trends in fishable biomass, it is important to understand the ecology of this phase of the life history (Cartwright et al. 2020). In this chapter, information from several sources were integrated to provide insight into the early life history of Snapper in South Australia. The sources included: the results from analysis of the microstructure of otoliths from juvenile Snapper sampled during an historic trawling program (Fowler and Jennings 2003); observations made during the rearing of Snapper larvae done recently at SAASC and in earlier studies elsewhere; the results from empirical studies that investigated the swimming ability of the larvae as they grew and developed; and information on the distribution and abundance of Snapper larvae determined through extensive regional plankton surveys.

Like most marine finfish, the early life history of Snapper involves a sequence of events and phases (summarised in Fig. 5.2). Spawning by the adult fish is followed by fertilisation of the eggs and their subsequent development over a day or two during which the embryo develops (Chapter 4). The larvae hatch as: simple, small, and undeveloped; with no functional mouth; the eyes lack retinal pigment; there is a continuous finfold that runs from the back of the head, around the tail, and anteriorly to the anus, with no fin rays; and no paired lateral fins. For several days, these small larvae are sustained endogenously through metabolism of the yolk and oil globule. This is a period of slow growth through which important developments occur, i.e., the eyes become functional, the jaws form and the larvae right themselves. These changes allow the larvae to undertake ‘first feeding’, i.e., the commencement of exogenous feeding. This event is associated with the formation of the first daily increment in the sagittae (Fowler and Jennings 2003). Several days after ‘first feeding’, swim bladder inflation occurs, which confers onto the larvae greater ability to control and maintain their position in the water column, thereby conserving energy.

Growth of the larvae was relatively slow until they were approximately 5 mm BL, when they underwent ‘flexion’ (the upward bending of the notochord tip, associated with formation of the caudal complex). Flexion was associated with development of caudal fin rays, whilst the fin rays for the dorsal, anal, and pectoral fins also became apparent. Based on the development of fins and increase in size, there was a significant improvement in swimming ability. The associated increase in feeding capacity may have at least partly contributed to the exponential increase in growth rate that occurred following flexion. Also, associated with subsequent development and growth, Snapper larvae gradually occurred deeper in the water column (Leis et al. 2006).

When the larvae attained approximately 10 mm BL, they were competent to undergo settlement. Through this latter part of their development, by which time all fins had developed and their swimming capabilities had advanced in terms of speed and endurance, the post-larvae became associated with the demersal environment and eventually underwent settlement. Whilst there was a range of estimates of sizes and ages at which settlement occurred, the annual mean size determined empirically was 9 – 10 mm CFL, with age ranging from 15 to 30 days (Chapter 8).

As Snapper larvae develop, the diagnostic morphological characteristics that are useful for their identification change with size and age (Cassie 1956, Kingsford and Atkinson 1994, Neira et al. 1998). The suite of changing characteristics include: morphometrics and overall body shape; the development of opercular and other head spines; the location and number of melanophores; and the numbers of pre-anal and post-anal myomeres. Based on our understanding of the changes in morphology that Snapper larvae undergo throughout their ontogenetic development, we were confident in being able to identify Snapper larvae in wild plankton samples.

5.4.2 Pre-settlement growth

From our understanding of the development and growth of otoliths in larval Snapper it was possible to reconstruct aspects of their growth throughout the larval phase. The important considerations included that during the period of endogenous feeding between hatch and first feed, no micro-increments formed in the otoliths. This lasted for the first two days. On the third day after hatching, the first increment was formed, which corresponded to the day of the first feed, i.e., the transition from endogenous to exogenous nutrition. Furthermore, there was a linear relationship between otolith size and somatic size, which meant that back-calculation could be used to reconstruct trajectories of somatic growth rates and growth patterns.

For Snapper from NSG, two periods of growth between first feed and settlement were evident. The initial period of slow, flat growth from first feed to flexion lasted up to approximately 10 days. Between flexion and settlement, the growth rates increased exponentially up to the age of approximately 22 days when settlement occurred. Through this time, the fins developed and so the swimming ability and endurance also increased considerably. Furthermore, the capability of maintaining orientated swimming also increased, suggesting that the larvae used sensory information to determine directionality whilst swimming.

5.4.3 Distribution and abundance of Snapper larvae

Throughout the latter part of 2020, the preserved ichthyolarvae from plankton samples collected in 2000 and between 2013 and 2020 were examined for Snapper larvae. Given the broad spatial scale of the plankton surveys and the volumes of water sampled, there were unexpectedly low numbers of Snapper larvae captured. In 2000, the plankton samples from 75 stations were extracted from a large total volume of water (Chapter 4). Then, across the four regional surveys undertaken in NSG in December in each of 2013, 2015, 2018 and 2019, a total of 863 plankton tows were done (Chapter 4, Table 4.3). These included 400 vertical plankton tows done in 2013 and 2015 that produced zero Snapper larvae. This result may have, at least partly, related to the low volumes of water that were sampled with the vertical tows (Chapter 4, Table 4.4). Nevertheless, although the 463 stations sampled in 2018 and 2019 with oblique plankton tows sampled considerably higher volumes of water, still only a single Snapper larva was captured.

Low numbers of Snapper larvae were also captured during the regional surveys in Gulf St. Vincent and Investigator Strait. The 418 vertical tows done in 2014 and 2015 produced 17,091 fish larvae but included only a single Snapper larva. Again, the low volume of water filtered may have contributed to this. In 2018 and 2020, the 441 oblique tows produced 35,872 ichthyolarvae. These included a total of 82 Snapper, two of which were captured in 2018 and 80 taken in 2020. The latter was by far the highest number recorded in any of our regional surveys. These larvae were geographically concentrated. They were captured at only 36 of the 265 sample stations and were in two areas, i.e., off the metropolitan coastline of Adelaide and in the western Investigator Strait. This survey also produced the highest absolute number of Snapper eggs at a relatively high density that were generally located in the vicinity of where the larvae were found (Chapter 4).

In 2020, the absolute number of Snapper larvae captured in Gulf St. Vincent and Investigator Strait was relatively high compared with other recent surveys. To compare with results from studies done elsewhere, the data were standardised to number.1000m^{-3} (Table 5.3). In 2020, the average catch rate across all stations in Gulf St. Vincent and Investigator Strait was 3.9 Snapper larvae.1000m^{-3} and ranged across stations from zero to 119.4 larvae.1000m^{-3}. For Port Phillip Bay (PPB), Victoria, a multi-year study considered the distribution and abundance of Snapper larvae during the spawning seasons of 2004 to 2009 (Hamer et al. 2010, Hamer et al. 2011, Murphy et al. 2012, 2013). Whilst far fewer stations in PPB were sampled than in Gulf St. Vincent and Investigator Strait, generally the absolute numbers of Snapper larvae captured were considerably higher (Table 5.3). For PPB, there was high inter-annual variation in catch rate, which varied from 1.0 to 34.0 Snapper larvae.1000m^{-3} (Table 5.3). The high annual catch rates in PPB were an order of magnitude higher than for Gulf St. Vincent and Investigator Strait.

During the 1980s, several other plankton sampling studies were undertaken. First, in the Hauraki Gulf, New Zealand, plankton sampling was done monthly during three consecutive reproductive seasons (Zeldis et al. 2005). The average monthly catch rates of Snapper larvae were generally at least an order of magnitude higher than recorded for Gulf St. Vincent and Investigator Strait (Table 5.3). The low catch rates in the Hauraki Gulf approximated the high rates in PPB, whilst the high catch rates in the Hauraki Gulf were an order of magnitude higher than those for PPB.

Table 5.3. Comparison of results from different studies that have sampled Snapper larvae or a closely related species.

Region	Year (month)	No. stations sampled	No. stations with Snapper larvae	Total number Snapper larvae	Ave. catch rate (no.1000m^{-3}) (+SD)	Max catch rate (no. 1000 m^{-3})
GSV (SA)	2020 Jan	265	36	80	3.9 (13.1)	119.4
PPB (Vic)	2004/05 (Dec/Jan)	49		534	34.0 (69.0)	367
	2005/06 (Dec/Jan)	58		25	1.0 (4.8)	26
	2006/07 (Dec/Jan)	54		92	4.4 (7.9)	35
	2007/08 (Dec/Jan)	55		298	15.0 (31.0)	170
	2008/09 (Dec/Jan)	50		574	29.0 (56.0)	345
Hauraki Gulf (NZ)	1985/86 Nov				20	
	1985/86 Dec				~10	
	1985/86 Jan				30	
	1986/87 Nov				30	
	1986/87 Dec				80	
	1986/87 Jan				40	
	1987/88Nov				320	
	1987/88Dec				300	
	1987/88Jan				330	
Shijiki Bay (Jap)	1982 (early May)	18	18			179.5
	1983 (early May)	18	18			110.0

The second relevant study in the 1980s was done in Japan for the Red Sea Bream (*Pagrus major*), a closely related species or sub-species of *Chrysophrys auratus* (Paulin 1990, Saunders 2009). For this species, plankton sampling was done in the vicinity of Shijiki Bay, Hirado Island, Kyushu, Japan. Whilst 35 stations were sampled regularly, 18 of these were located outside the bay (Tanaka 1985). In early May in each of 1982 and 1983, larval Red Sea Bream were collected at all 18 sampling stations for which the highest catch rates were 179.5 and 100.0 larvae .1000m^{-3}, respectively. The significance of this is that there was an of area of ocean that was >1,000 km^{2} outside of Shijiki Bay throughout which all stations that were sampled from year-to-year consistently produced catches of Red Sea Bream larvae. Such spatial and inter-annual consistency was clearly not a feature of the distribution and abundance of Snapper larvae in South Australia.

Each of the studies done in PPB, Hauraki Gulf and Japan demonstrated inter-annual variation in abundances of Snapper larvae. For the Victorian and New Zealand studies, the average larval abundances recorded in some years were at least one or two orders of magnitude higher than the highest regional abundance that was recorded for Gulf St. Vincent and Investigator Strait. Overall, the empirical observations and comparisons with results for other places, suggest that in 2000 and throughout 2013 to 2020, the waters of NSG, Gulf St. Vincent and Investigator Strait were depauperate of Snapper larvae. Such low numbers of Snapper larvae in South Australian waters could relate to poor egg production and/or poor survivorship of the recently hatched larvae. There is some evidence that the former hypothesis is at least partly responsible in that, as demonstrated in Chapter 4, the estimates of absolute numbers of Snapper eggs and their densities were considerably lower than obtained in studies undertaken elsewhere.

5.5 References

Battaglene, S.C., Talbot, R.B. (1992). Induced spawning and larval rearing of snapper, *Pagrus auratus* (Pisces: Sparidae), from Australian waters. New Zealand Journal of Marine and Freshwater Research 26: 179-183.

Campana, S.E. (1990). How reliable are growth back-calculations on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47: 2219-2227.

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

Cartwright, I., McPhail, J., Knuckey, I., Smith, T., Rayns, N., Steer, M. (2020). National Snapper Workshop – Rebuilding our iconic Snapper stocks. Final report to FRDC (Project No. 2019/085). 58pp.

Cassie, R.M. (1956). Early development of the Snapper, *Chrysophrys auratus* Forster. Transactions of the Royal Society of New Zealand. Vol 83 (4): 705-713.

Clark, D.L., Leis, J.M., Hay, A.C., Trnski, T. (2005). Swimming ontogeny of larvae of four temperate marine fishes. Marine Ecology Progress Series 292: 287-300.

Crossland, J. (1980). The number of Snapper (Forster), in Hauraki Gulf, based on egg surveys in 1974-75 and 1975-76. Fisheries Research Bulletin No. 22, Fisheries Research Division, Ministry of Agriculture and Fisheries, New Zealand.

Fowler, A.J., 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., McGlennon, D. (2011). Variation in productivity of a key snapper, *Chrysophrys auratus*, fishery related to recruitment and fleet dynamics. Fisheries Management and Ecology 18: 41-423.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E., Jackson. (2010). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-2. SARDI Research Report Series No. 473. 109pp.

Fowler, A.J., Hamer, P.A., Kemp, (2017). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely-dispersed, coastal fishery species. Fisheries Research 189: 77-94.

Fowler, A.J., Smart, J., McGarvey, R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

Hamer, P.A., Jenkins, G.P., Acevedo, S. (2010). Importance of spawning in Port Philip Bay to local snapper stocks. Fisheries Victoria Research Branch No. 37, Queenscliff.

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Hoss, D.E., Checkley, D.M., Settle, L.R. (1989). Diurnal changes in larval Atlantic menhaden (*Brevoortia tyrannus*). Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 191: 105-111.

Hunter, J.R., Sanchez, C. (1976). Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fishery Bulletin 74: 847-855.

Jackson, G., Cheng, Y.W., Wakefield, C.B. (2012). An evaluation of the daily egg production method to estimate spawning biomass of Snapper (*Pagrus auratus*) in inner Shark Bay, Western Australia, following more than a decade of surveys 1997-2007. Fisheries Research 117-118: 22-34.

Leis, J.M. (2007). Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. Marine Ecology Progress Series 347: 185-193.

Leis, J.M. (2010). Ontogeny of behaviour in larvae of marine demersal fishes. Ichthyology Research 57: 325-342.

Leis, J.M. (2020). Measurement of swimming ability in larval marine fishes: comparison of critical speed and *in situ* speed. Marine Ecology Progress Series 650: 201-215.

Leis, J.M., Hay, A.C., Trnski, T. (2006). *In situ* ontogeny of behaviour in pelagic larvae of three temperate, marine, demersal fishes. Marine Biology 148: 655-669.

Leis, J.M., Siebeck, U., Dixson, D. (2011). How Nemo finds home: the neuroecology of dispersal and of population connectivity in larvae of marine fishes. Integrative and Comparative Biology 51: 826-843.

McGlennon, D. (2003). The fisheries biology and population dynamics of Snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. PhD Thesis, University of Adelaide, Adelaide, South Australia. 212pp.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2012). Interannual variation in larval survival of snapper (*Chrysophrys auratus*, Sparidae) is linked to diet breadth and prey availability. Canadian Journal of Fisheries and Aquatic Sciences 69: 1340-1351.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2013). Interannual variation in larval abundance and growth in snapper *Chrysophrys auratus* is related to prey availability and temperature. Marine Ecology Progress Series 487: 151-162.

Neira, F.J., Miskiewicz, A.G., Trnski, T. (1998). Larvae of temperate Australian fishes. Laboratory guide for larval fish identification. University of Western Australia Press.

Pankhurst, P.M., Montgomery, J.C., 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.

Partridge, G.J., Jenkins, G.I., Frankish, K.R. (2003). Hatchery manual for the production of Snapper (*Pagrus auratus*) and Black Bream (*Acanthopagrus butcheri*). WestOne Publishing, Perth.

Saunders, R.J. (2009). The reproductive biology and recruitment dynamics of snapper, *Chrysophrys auratus*. PhD Thesis, University of Adelaide, Adelaide, South Australia. 154pp.

Saunders, R.J., Fowler, A.J., Gillanders, B.M. (2012). The spawning dynamics of snapper (*Chrysophrys auratus*) in northern Spencer Gulf, South Australia. New Zealand Journal of Marine and Freshwater Research 46: 491-510.

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.

Wakefield, C.B. (2010). Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. Journal of Fish Biology 77: 1359-1378.

Zeldis, J.R., Oldman, J., Ballara, S.L., Tichards, L.A. (2005). Physical fluxes, pelagic ecosystem structure and larval fish survival in Hauraki Gulf, New Zealand. Canadian Journal of Fisheries and Aquatic Sciences 62: 593-610.

5.6 Appendices

5.6.1 Microstructure of juvenile Snapper otoliths

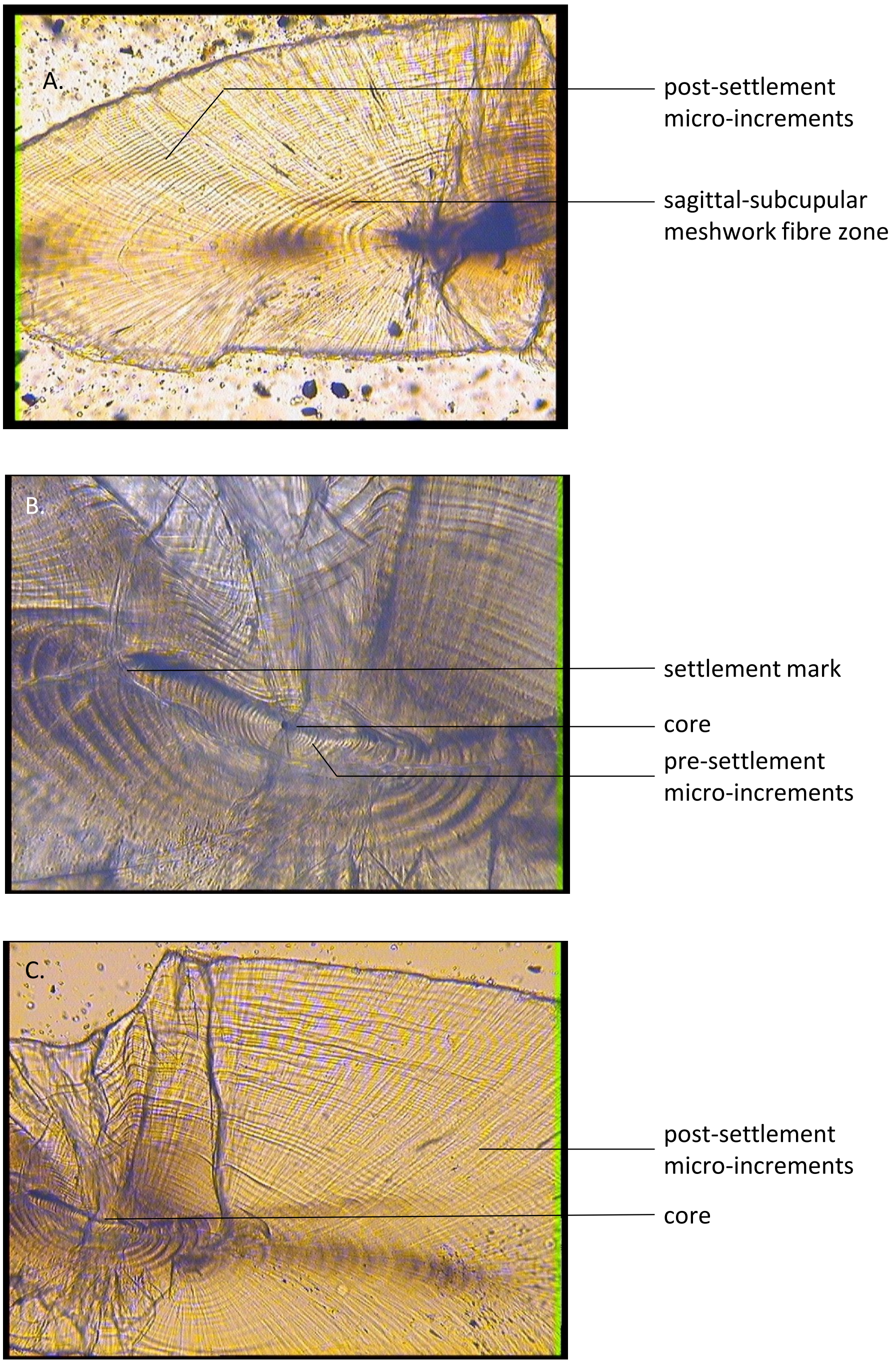


Fig. A5.1. Photomicrographs of the microstructure in transverse sections of the sagittae of juvenile Snapper sampled from NSG. A. Some pre-settlement and post-settlement microincrements towards the ventral edge. B. high-powered view of the core region showing, pre-settlement and post-settlement microincrements. C. View of the proximal surface and part of the sulcus, showing the centrally-located core and some post-settlement microincrements towards the ventral edge.

5.6.2 Development of Snapper larvae

Following is a description of the development of Snapper larvae through the first few days after hatching. The descriptions are based on those of Cassie (1956), and observations from fresh and preserved reared specimens at SAASC.

1. Newly hatched larvae (Fig. A5.2):
    a. length is approximately 2.2 – 2.6 mm BL (n = 5);
    b. preflexion;
    c. eyes lack retinal pigment;
    d. straight gut;
    e. large yolk sac with posterior positioned oil globule;
    f. median fin is continuous from the back of the head dorsally to around the tail to the anus ventrally;
    g. formalin-preserved specimens show reddish, stellate melanophores on the head and dorsally. Live specimens show several large melanophores on the hindbrain, over the nape, and along the length of the body, with a series of small melanophores along the dorsal midline of the trunk.

2. Day-2 larvae (Fig. A5.3):
    a. length has increased marginally to 2.6 – 3.2 mm BL (n = 5);
    b. preflexion;
    c. yolk sac and oil globule are considerably reduced in size, and separated from the gut and anus;
    d. median fin is still evident
    e. live specimens show similar pigmentation to newly hatched larvae.

3. Day-3 larvae (from Cassie 1956)
    a. average length developed to 3.2 mm BL;
    b. preflexion;
    c. yolk sac further reduced;
    d. jaws have begun to form although mouth is not yet functional;
    e. retina has begun to darken, although the lens remains visible;
    f. small pectoral fins have begun to develop.

4. Day-4 (from Cassie 1956)
    a. little change in length;
    b. preflexion;
    c. yolk sac and oil globule have been fully metabolised;
    d. jaws completely developed and functional;
    e. gut has increased in size and become convoluted;
    f. retina has become pigmented to a deep black;
    g. pectoral fins have enlarged and are functional;
    h. median fin is still thin and transparent, but fin rays are becoming evident.

The following is a summary of the description of the further development of Snapper larvae from Neira et al. (1998). The focus here is on those features that proved useful for identifying Snapper larvae from the wild plankton samples. Figures A5.4 to A5.16 show the development of the larvae from 10-days of age when they were approximately 3.0 mm BL to pre-recruits that were >30 days old and >8.0 mm BL in size.

1. Diagnostic characters
    a. 8 – 10 pre-anal myomeres and 14-17 post-anal myomeres;
    b. preflexion and flexion larvae have elongate posterior preopercular spines whilst flexion larvae also have supracleithral and interopercular spines;
    c. one large internal melanophore located over the nape (dorsal region of trunk immediately posterior to the head);
    d. two large melanophores ventrally on gut;
    e. one to three melanophores under notochord tip.

2. Description of larvae
    a. body depth (BD) measured at the pectoral fin base is moderate, i.e. 24-34% of BL;
    b. head length (HL) measured from the tip of the upper jaw to the operculum is moderate in preflexion and flexion larvae (HL 25-32%), and moderate to large in postflexion larvae (HL 30-36%);
    c. dorsal profile is steep;
    d. small teeth along both jaws from early flexion stage;
    e. small opercular and other head spines in preflexion and flexion larvae and other spines form subsequent to flexion;
    f. gut moderate in preflexion and flexion larvae, long in postflexion larvae, coiled and compact;
    g. small gas bladder located above the foregut.

3. Pigmentation
    a. preflexion larvae – 0-3 melanophores over mid brain;
    b. one melanophore on isthmus;
    c. a few additional melanophores on gut in postflexion larvae;
    d. preflexion larvae have a series of 7-17 melanophores along the ventral midline of the tail;
    e. from 7.7 mm BL, additional melanophores along anal fin base and ventral midline of caudal peduncle;
    f. from 9.2 mm BL, melanophores on membrane between dorsal fin spines along dorsal fin base;
    g. near settlement, broad vertical bands of pigment occur laterally on the trunk and tail;
    h. preflexion larvae – one to three melanophores under notochord tip;
    i. postflexion larvae – melanophores remain along lower portion of the caudal fin base;
    j. one large melanophore over nape is gradually obscured by muscle tissue with growth.

Fig. A5.2. Photograph of Snapper larva on the day when hatched.

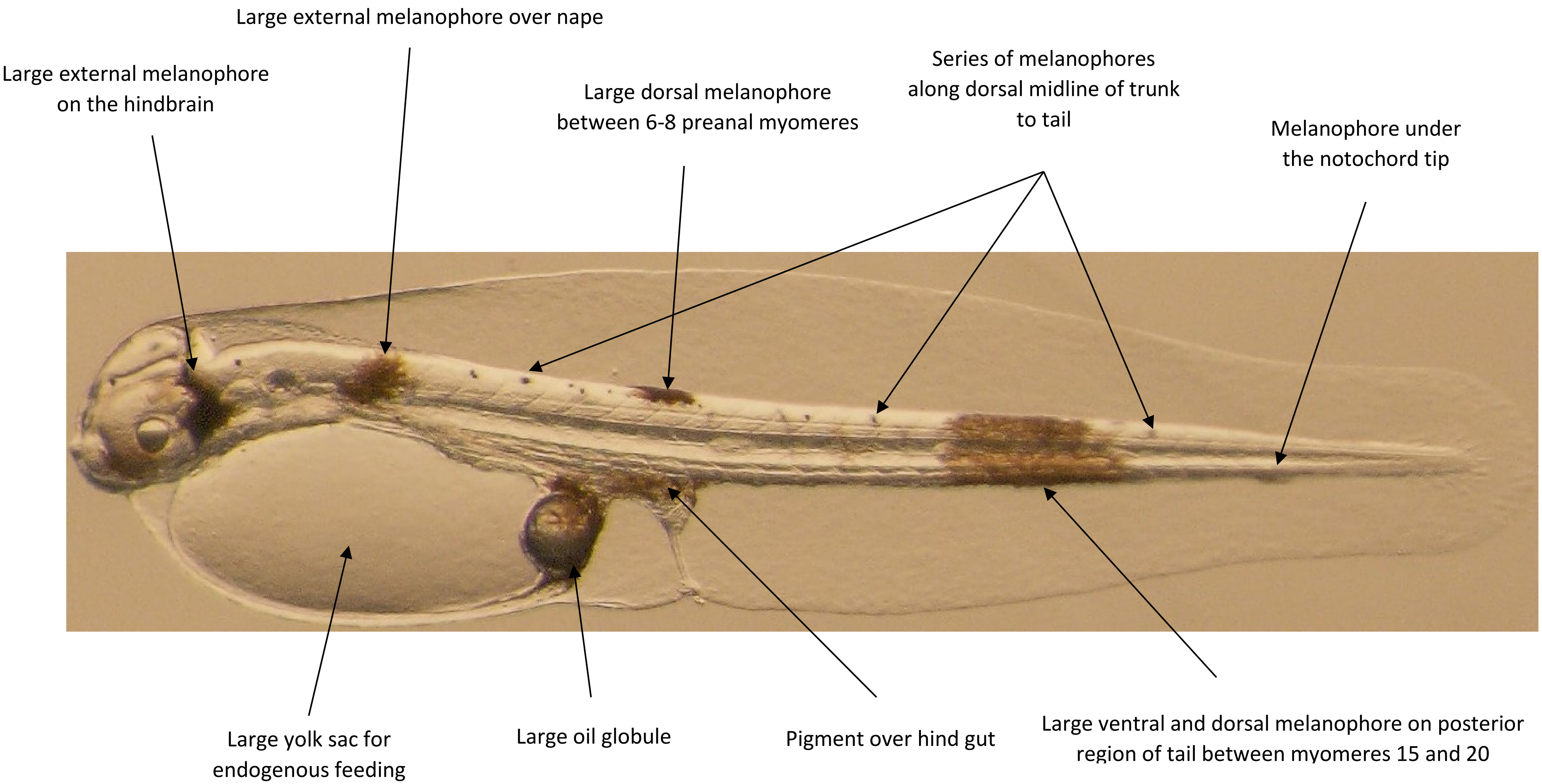


Fig. A5.3. Photograph of Snapper larva on the day after hatching.

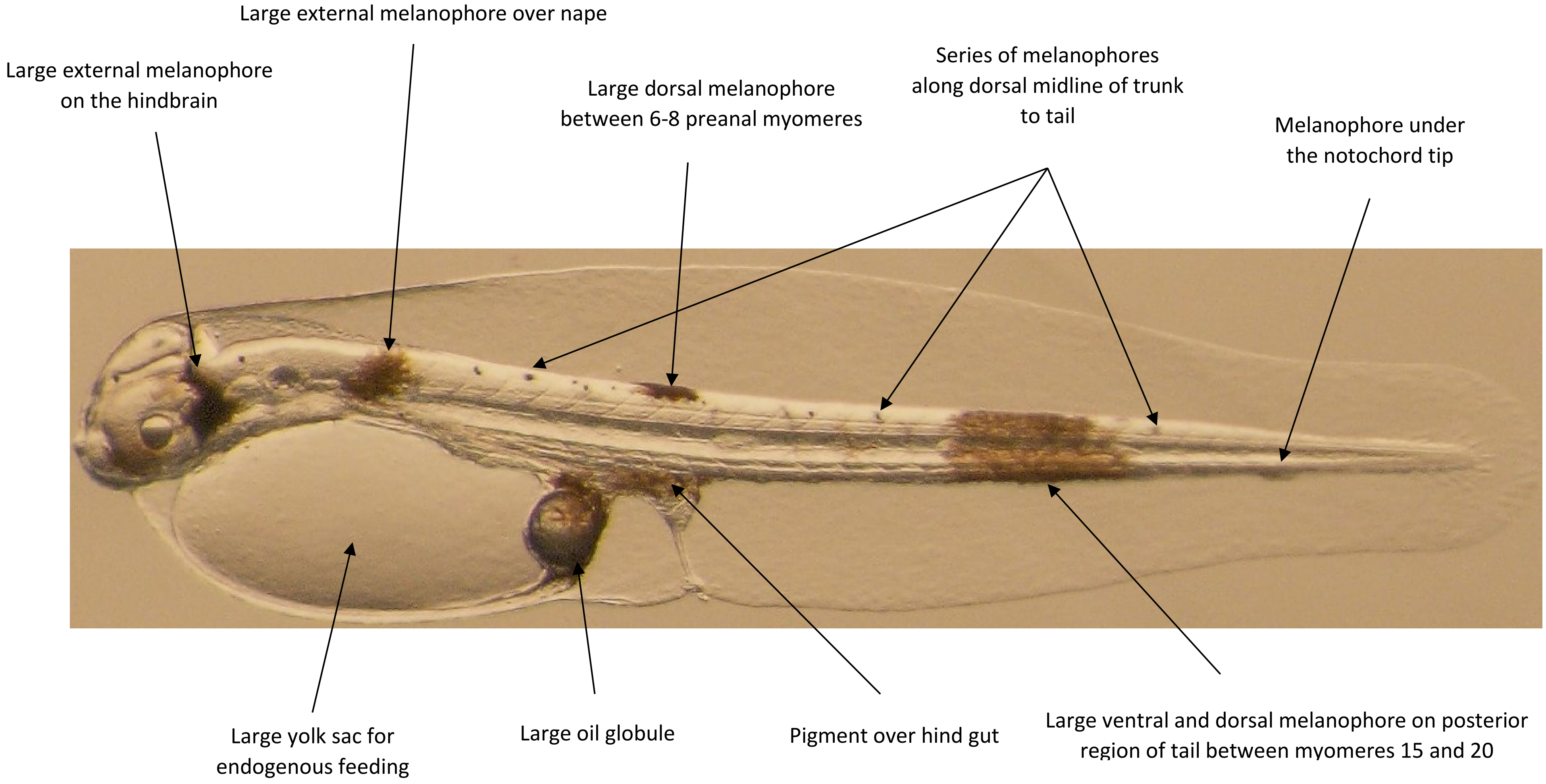


Fig. A5.4. Photograph of Snapper larva 10 days after hatching.

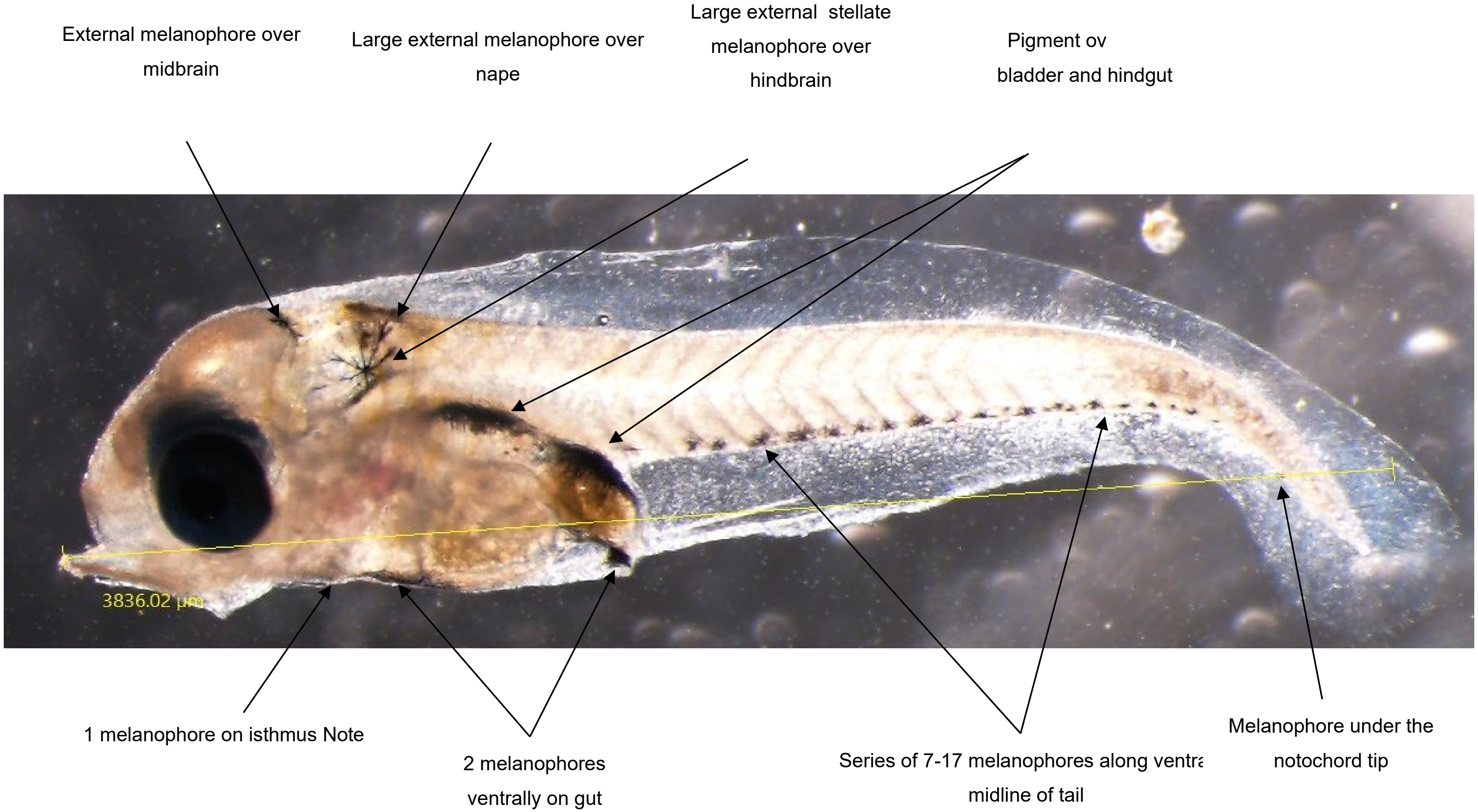


Fig. A5.5. Photograph of Snapper larva 12 days after hatching.

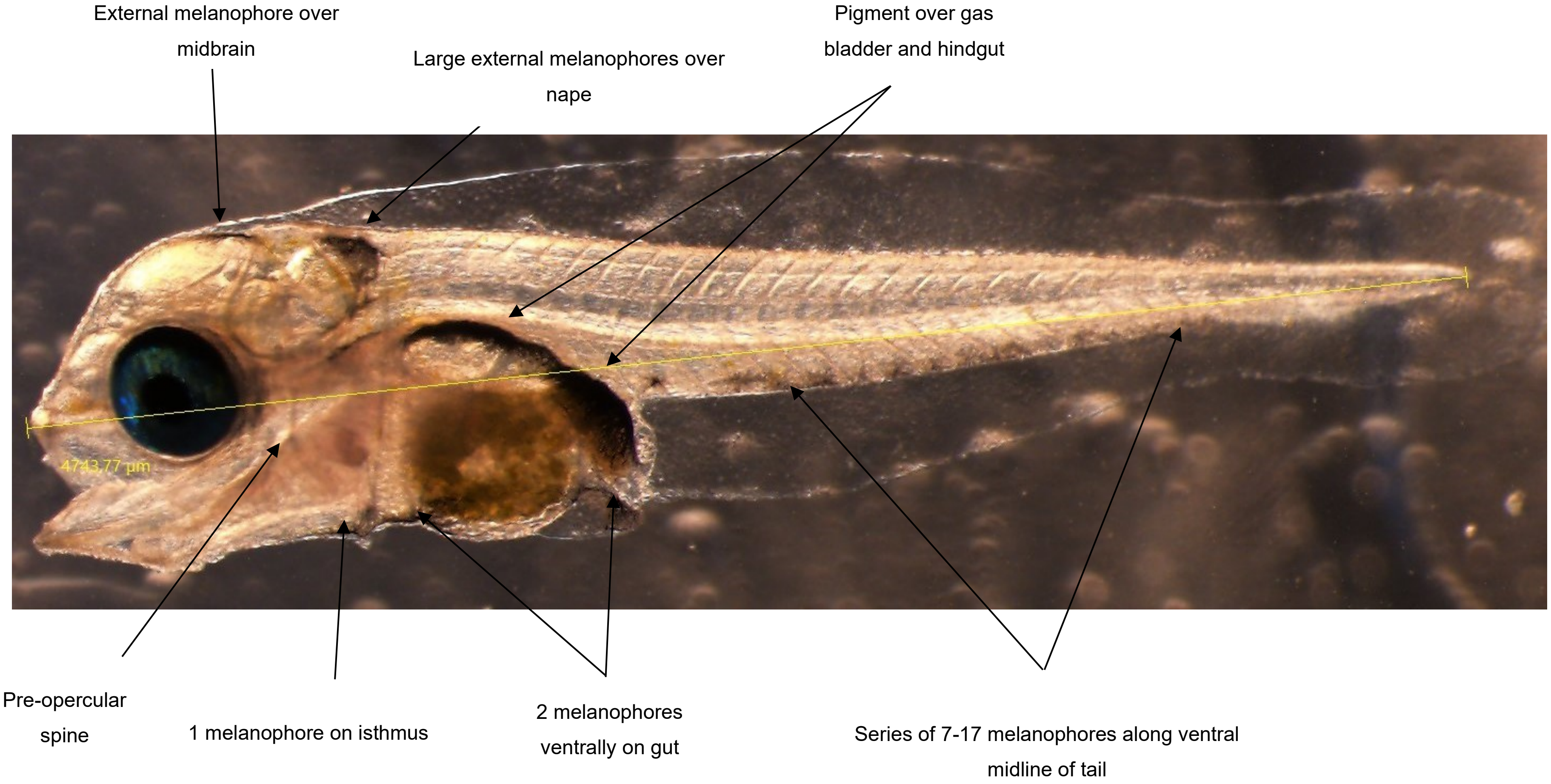


Fig. A5.6. Photograph of Snapper larva 13 days after hatching.

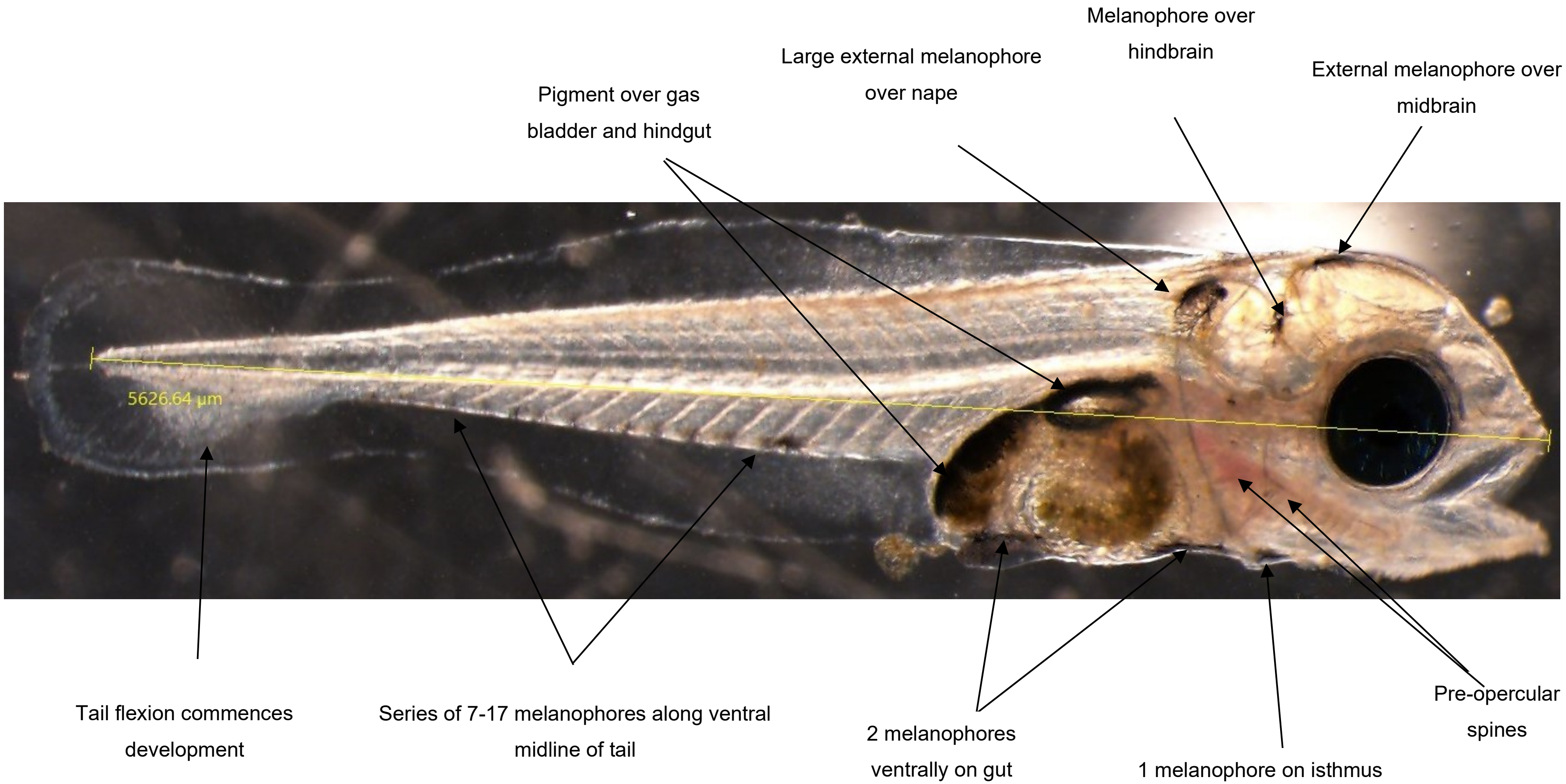


Fig. A5.7. Photograph of Snapper larva 14 days after hatching.

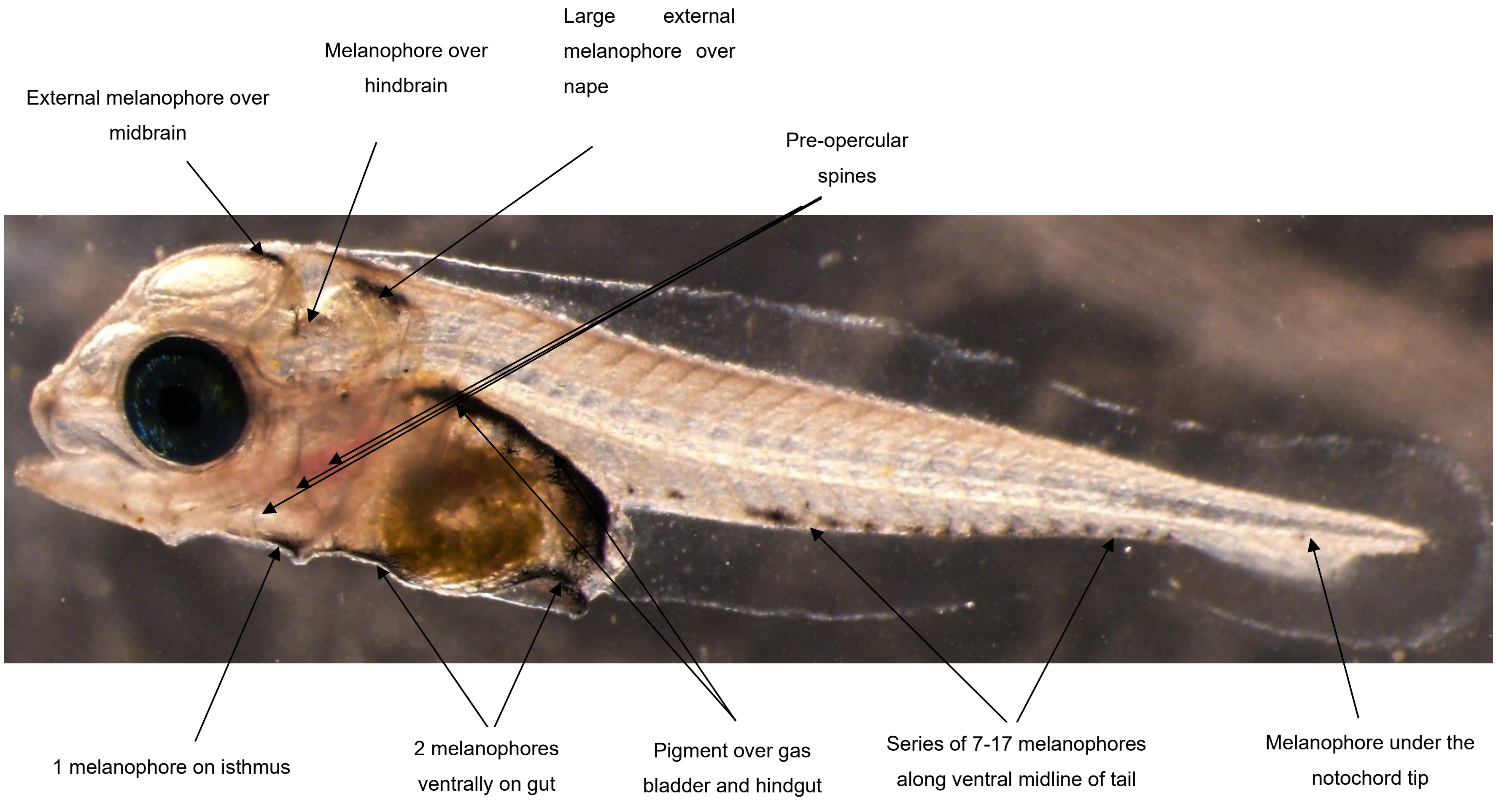


Fig. A5.8. Photograph of Snapper larva 17 days after hatching.

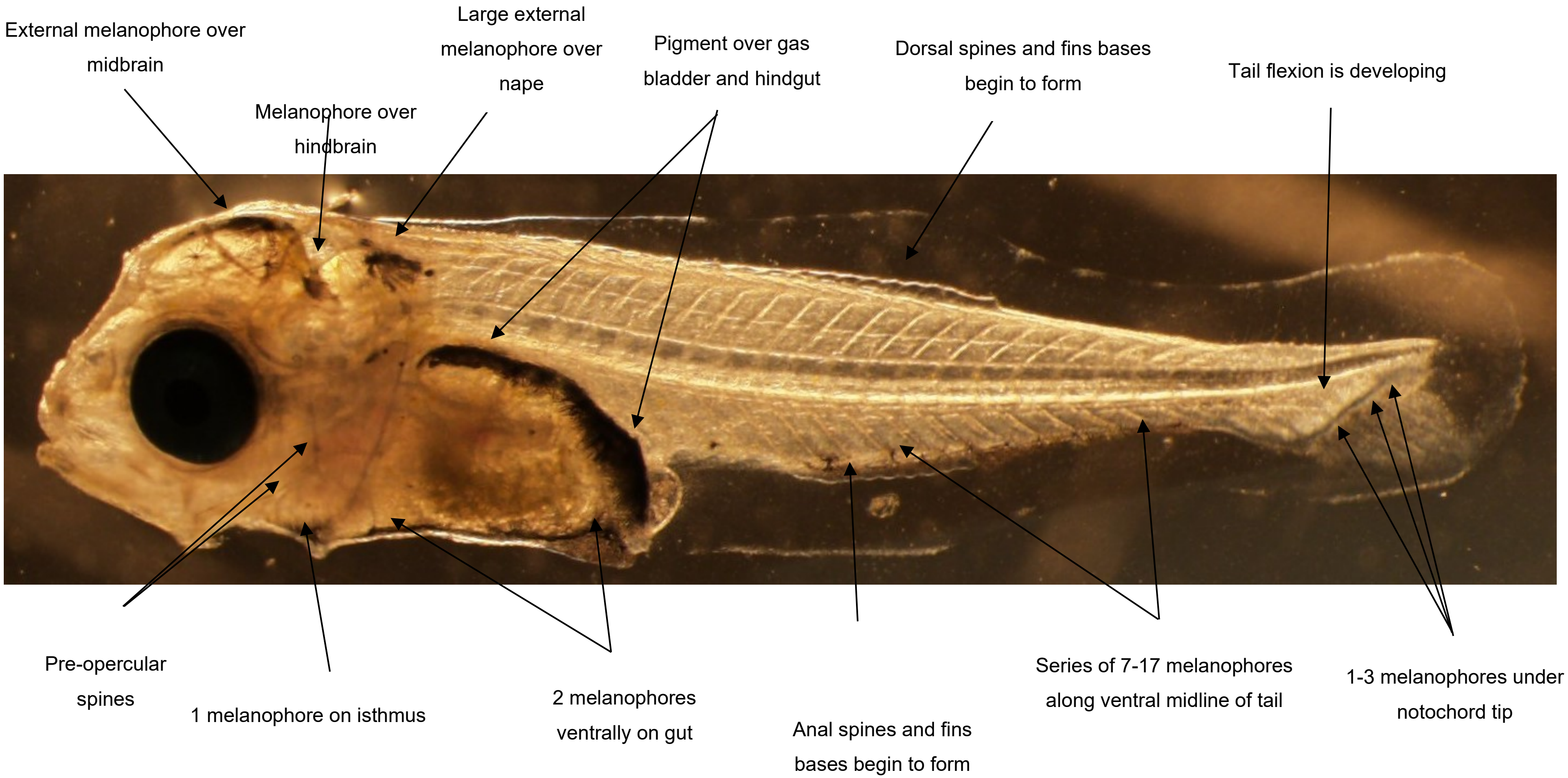


Fig. A5.9. Photograph of Snapper larva 18 days after hatching.

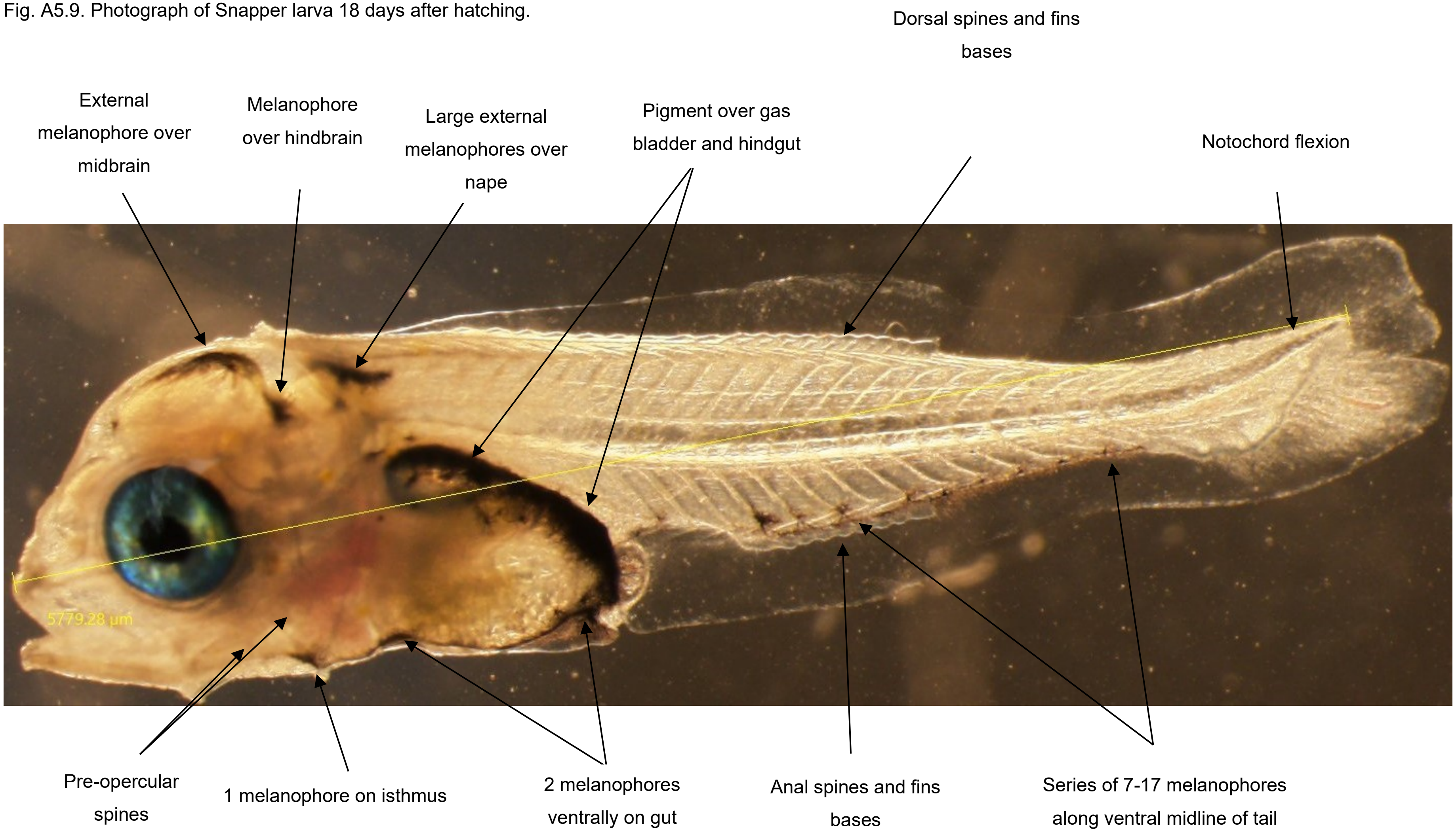


Fig. A5.10. Photograph of Snapper larva 19 days after hatching.

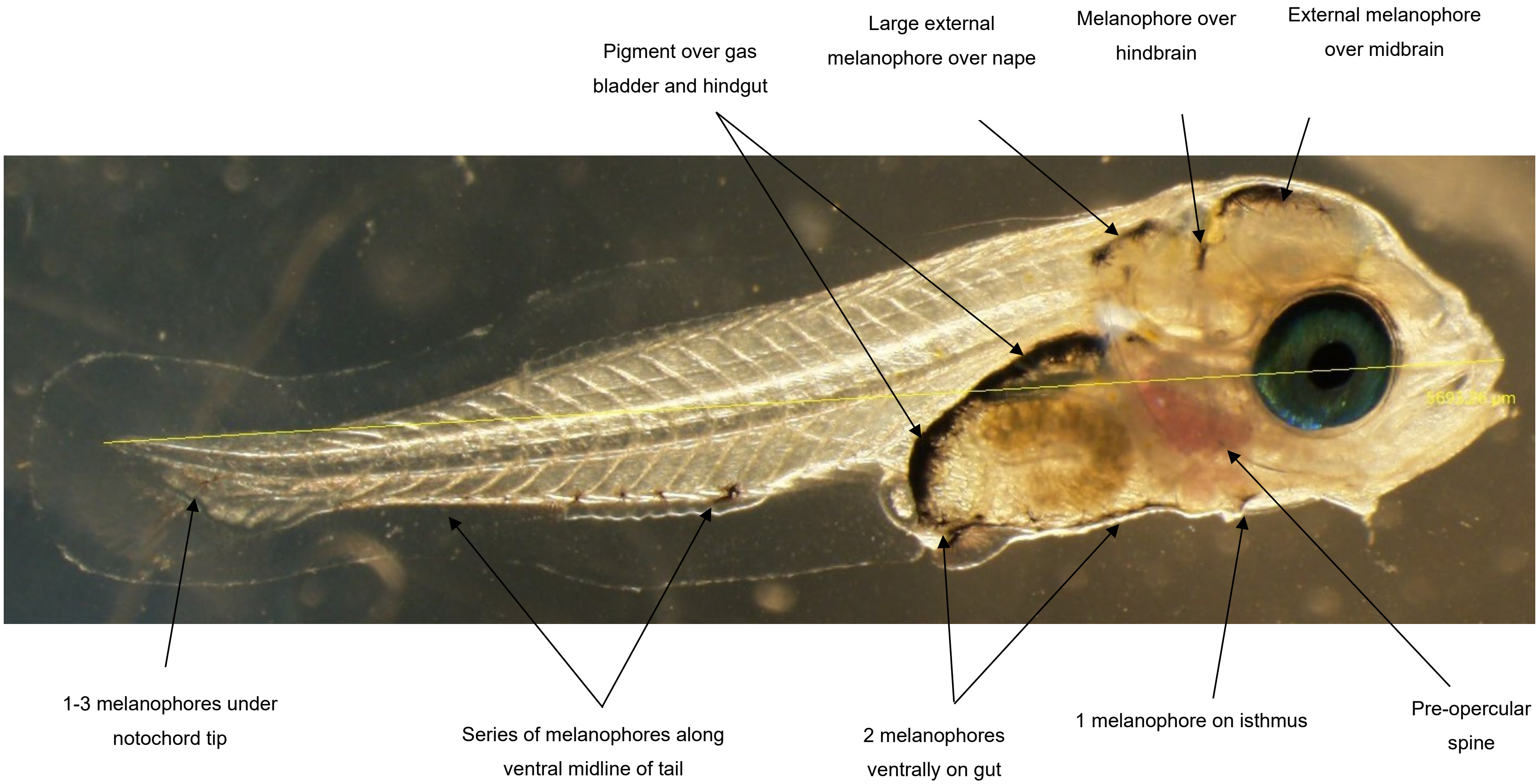


Fig. A5.11. Photograph of Snapper larva 20 days after hatching.

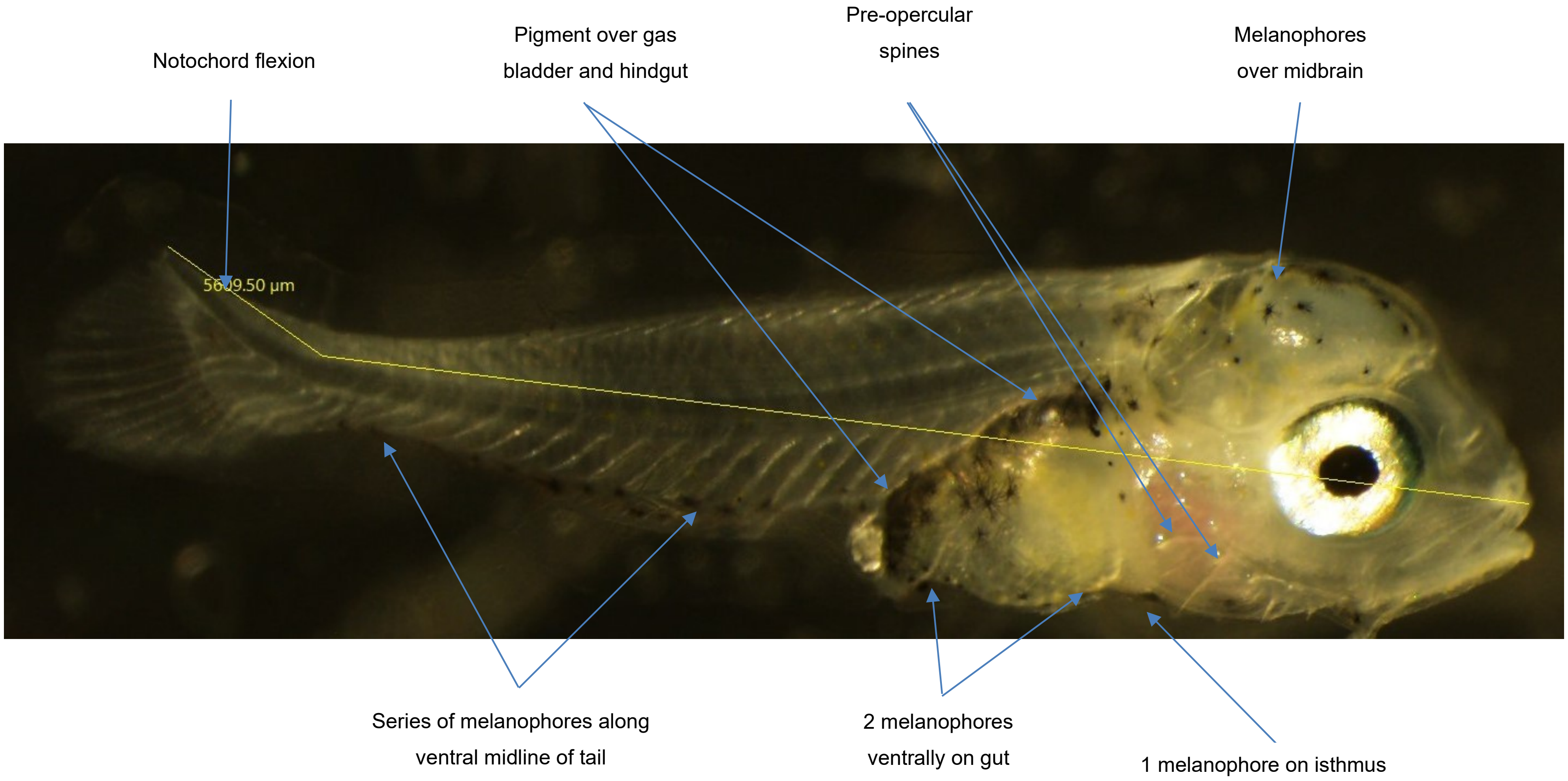


Fig. A5.12. Photograph of Snapper larva 21 days after hatching.

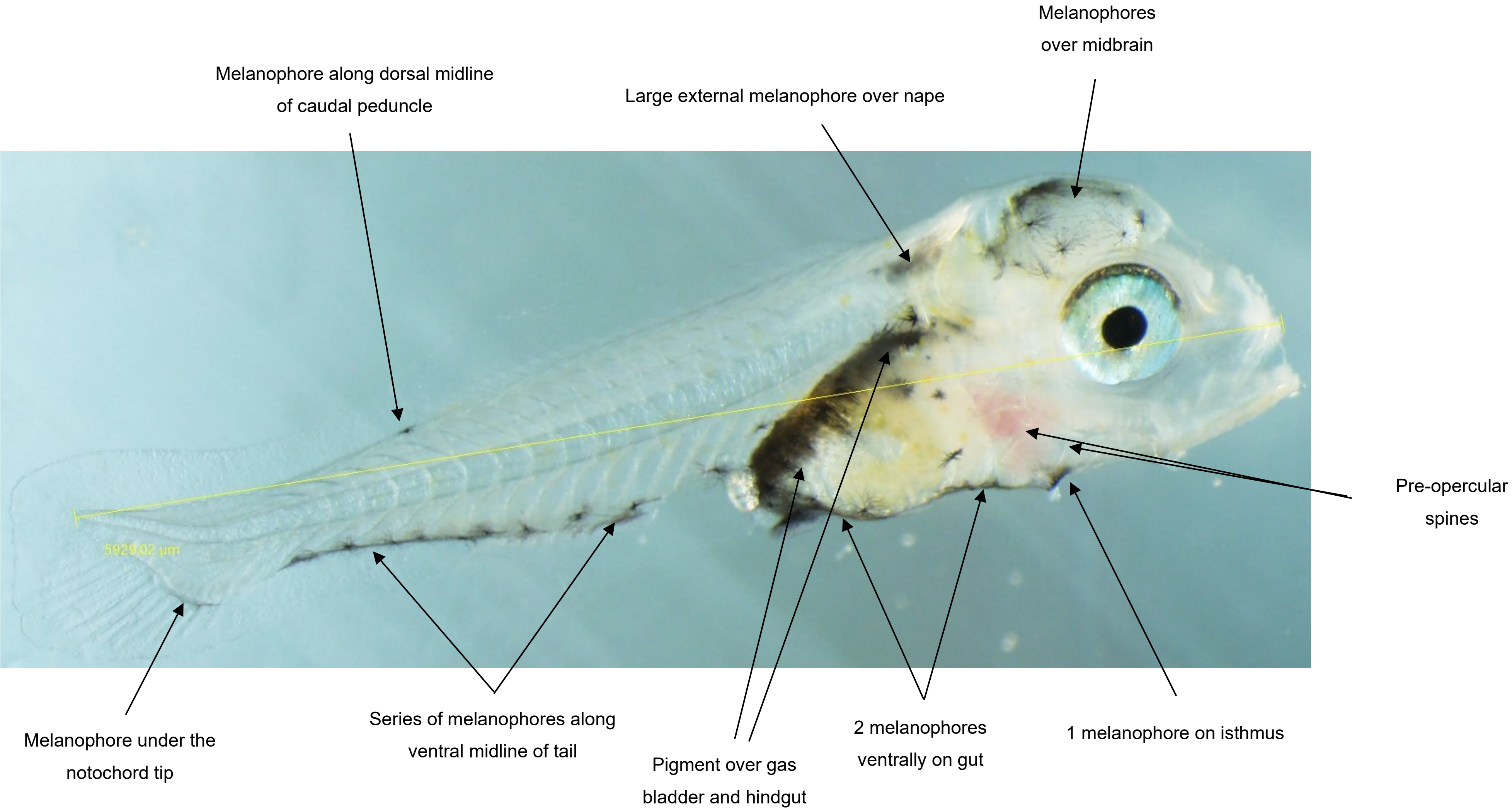


Fig. A5.13. Photograph of Snapper larva 24 days after hatching.

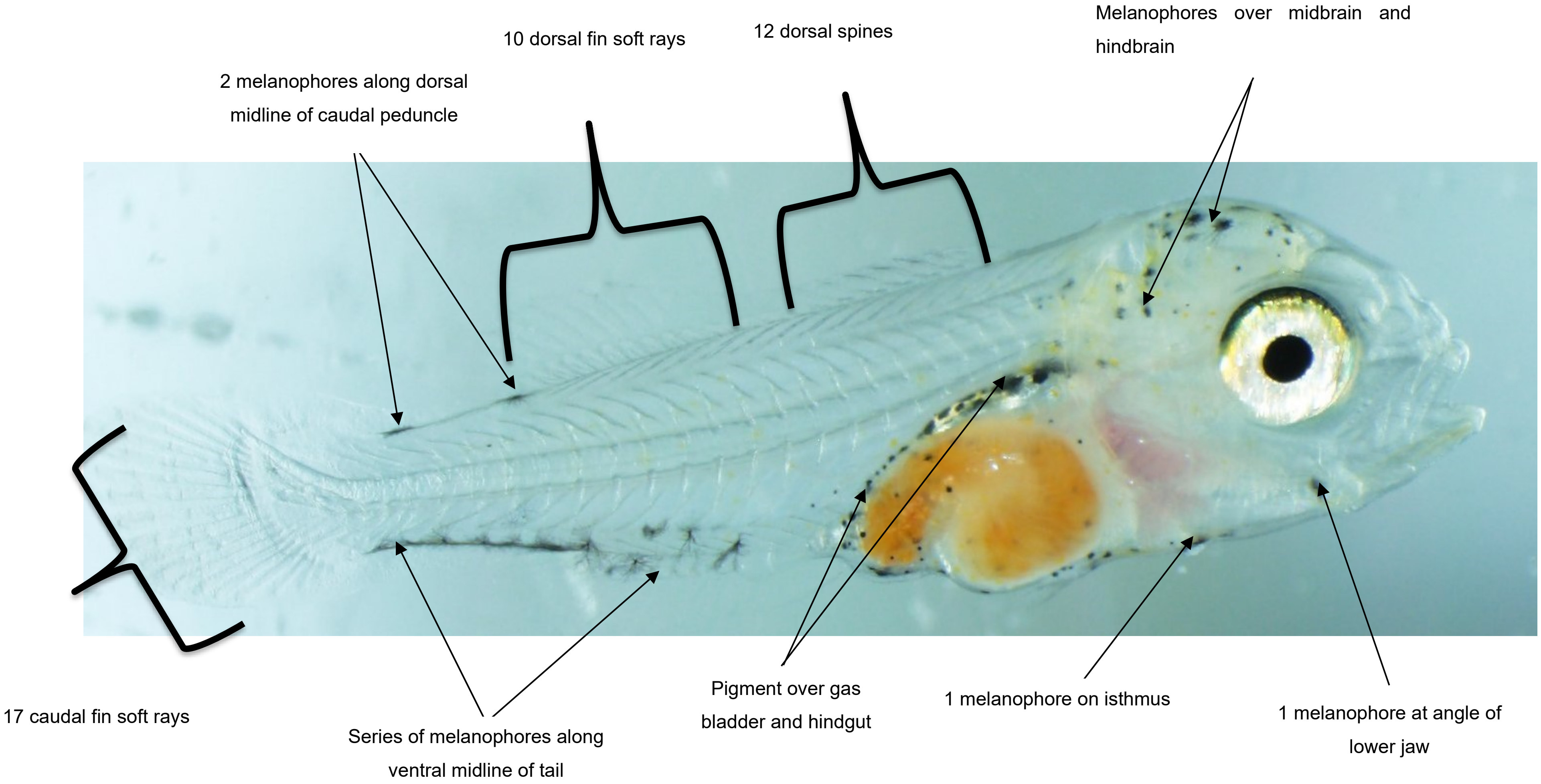


Fig. A5.14. Photograph of Snapper post-larva 31 days after hatching.

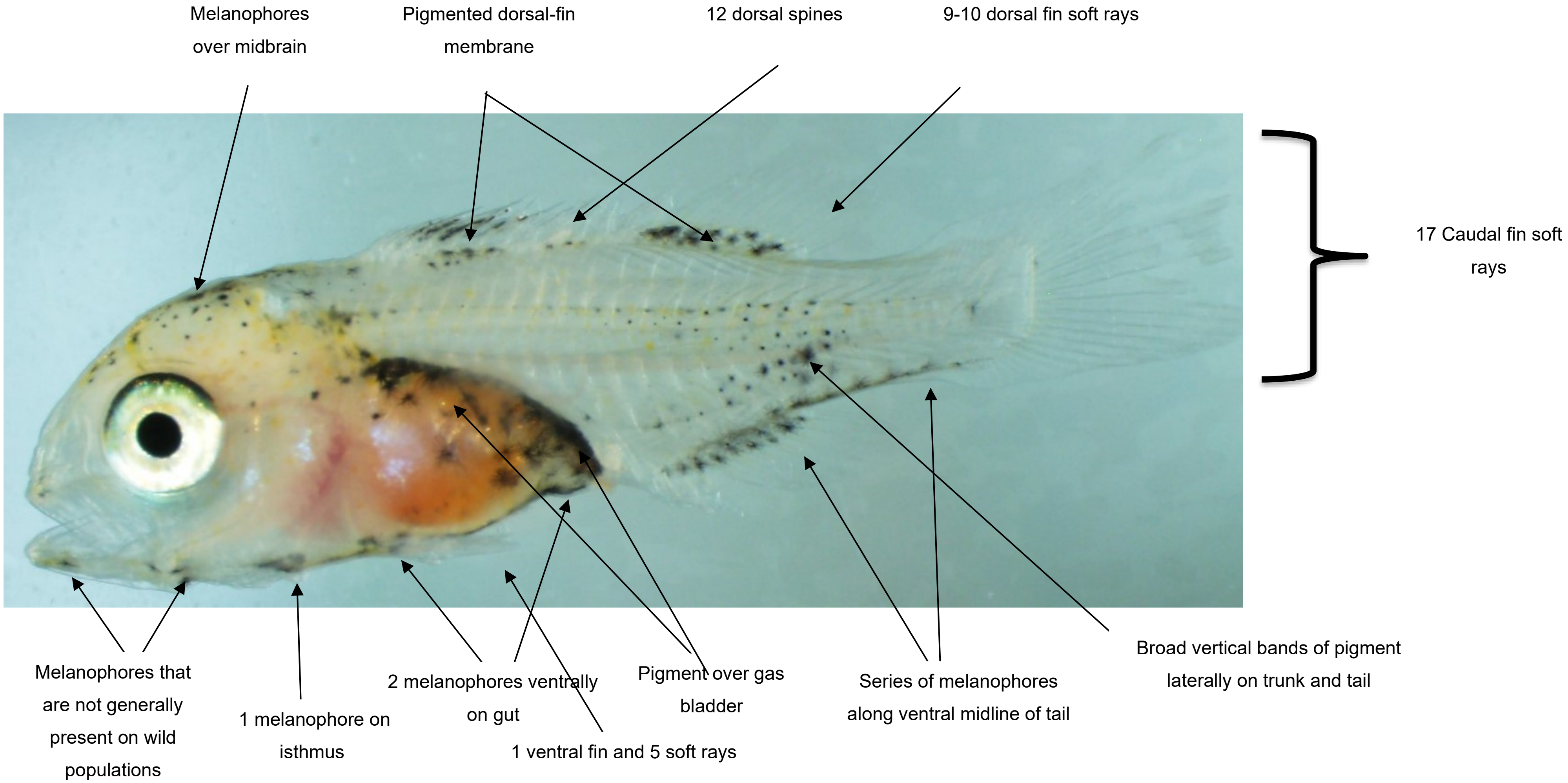


Fig. A5.15. Photograph of Snapper post-larva 31 days after hatching.

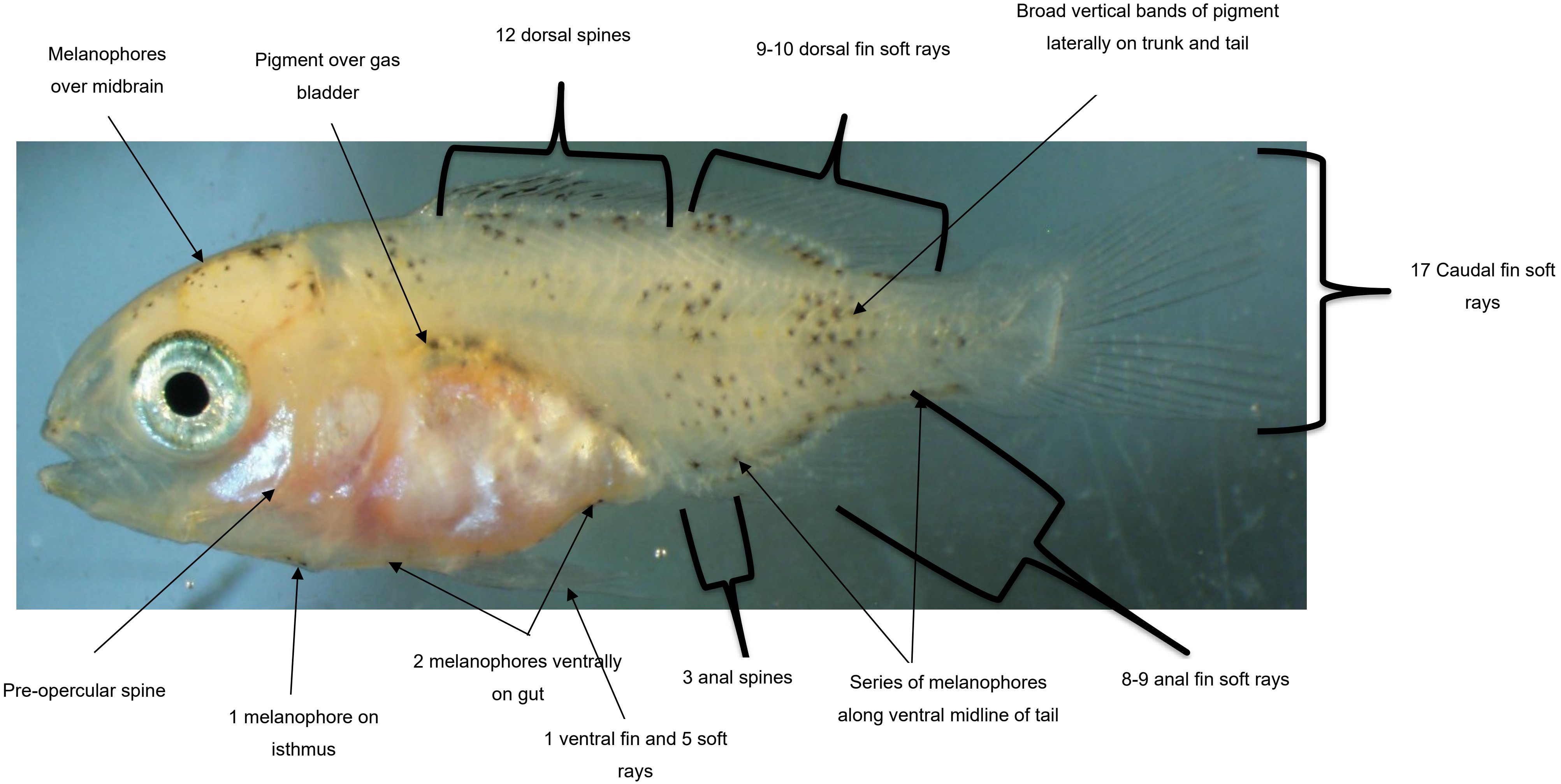
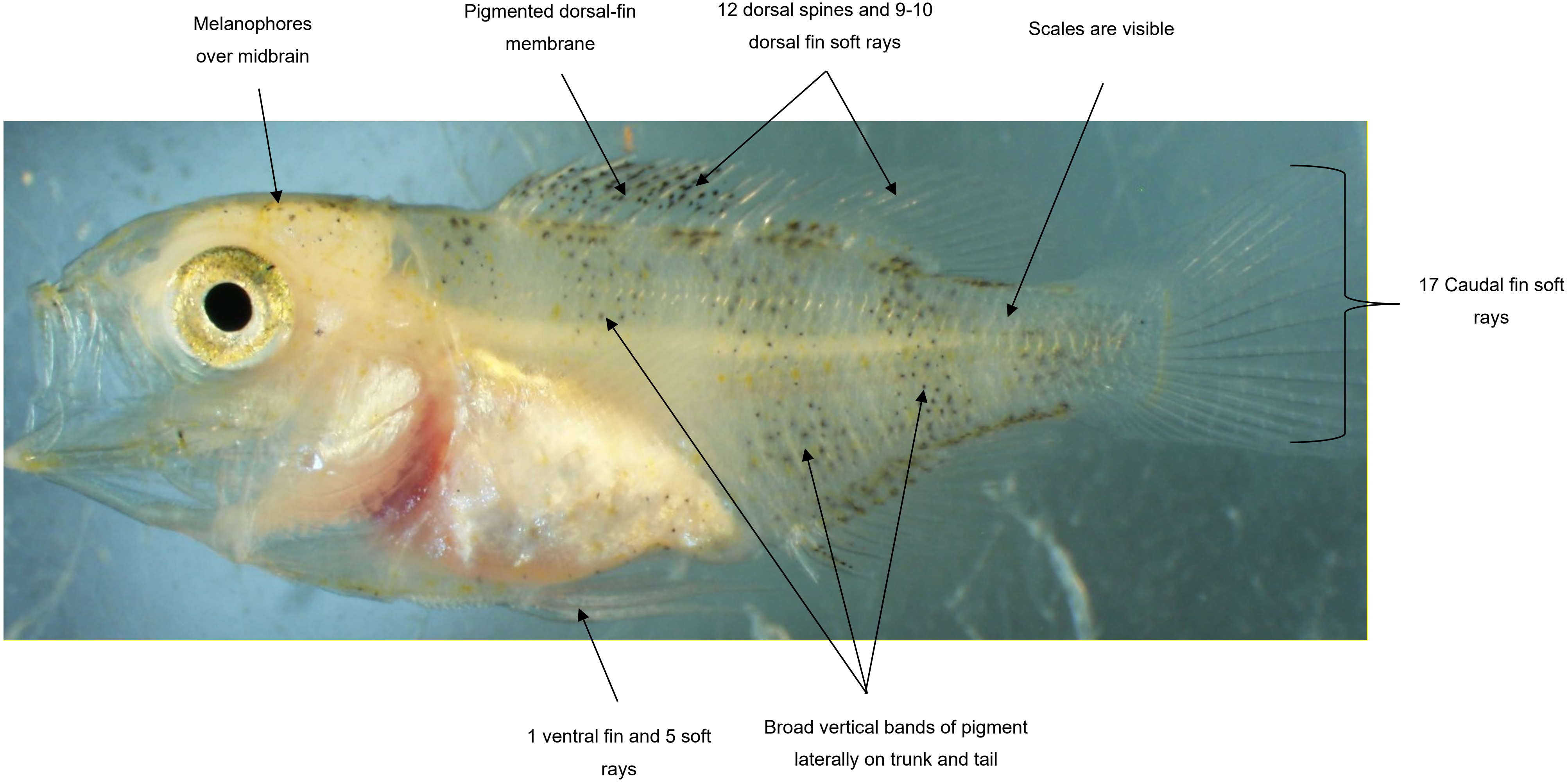


Fig. A5.16. Photograph of Snapper post-larva 33 days after hatching.



6. DISTRIBUTION AND ABUNDANCE OF JUVENILE SNAPPER

Anthony Fowler

6.1 Introduction

The population dynamics and fishery productivity of Snapper in South Australia are fundamentally driven by inter-annual variation in recruitment of the 0+ year class (Chapter 9, McGlennon and Jones 1997, Fowler and Jennings 2003, Fowler et al. 2005, 2007, Fowler and McGlennon 2011). Snapper populations in South Australia are characterised by having distinct strong and weak age classes that relate to variation in recruitment of the 0+ Snapper and the resulting variation in year-class strength (McGlennon et al. 2000, Fowler and Jennings 2003). The occasional strong year class can sustain the fishery through periods of numerous years that are characterised by poor to average recruitment. For example, the recovery of the fishery in Spencer Gulf through the mid-to-late 1990s, evident in increases in catches and catch rates up to record levels around 1999 and 2000, were largely related to an exceptional year class that recruited as 0+ fish in 1991 (Fowler et al. 2005, 2010, Fowler and McGlennon 2011).

Since the productivity of the regional South Australian Snapper fisheries are largely determined by variable recruitment, then having an accurate annual index of recruitment could be a good predictor of future adult biomass and fishery productivity (Cartwright et al. 2020). This would be a valuable contribution to stock assessments and provide a strong basis for a dynamic approach to fishery management. One aim of SARDI's Snapper research program through the 2000s was to develop some understanding about the variability in recruitment. This has involved addressing two objectives: describing the spatial and temporal patterns of recruitment of 0+ fish in Northern Spencer Gulf (NSG); and elucidating aspects of the early life history and larval and juvenile ecology.

To address the first objective of describing the spatial and temporal patterns of recruitment it was necessary to determine the appropriate stage of the early life history to sample and to determine where, when, and how to sample. Whilst the sampling and data on the distribution and abundance of Snapper eggs and larvae were dealt with in Chapters 4 and 5, this chapter describes two types of studies that have provided spatial and temporal information on the juvenile stage of the life history. The purpose of this chapter was to review such studies done to date, their methodologies and to summarise their findings. The specific objectives addressed here were: to present a chronology of the regional 0+ surveys that have been undertaken in NSG, comparing amongst the methods used and the results obtained regarding the distribution and abundance of juvenile

Snapper; and to summarise the spatial and temporal information on juvenile Snapper that has come from the chronology of by-catch surveys from the Spencer Gulf Prawn Fishery.

6.2 Materials and methods

6.2.1 History of trawl-based surveys for juvenile Snapper

Some level of sampling for juvenile Snapper was done every year between 1999 and 2010 (Fowler et al. 2010), and then again in 2021 (Rogers et al. 2021). Whilst all surveys involved trawling from the MRV *Ngerin*, they differed with respect to: the specific details in sampling methodology; the extent of the region surveyed; the numbers of and spatial distribution of sampling stations; and their timing with respect to the reproductive season. Here, a chronology is presented of the different studies that describes the methodological approaches and summarises their results.

6.2.2 Chronology of studies on by-catch from the Spencer Gulf Prawn Fishery

Through the 1990s and 2000s, several studies documented the by-catch from stock assessment trawl surveys undertaken by the Spencer Gulf Prawn Fishery. The survey data provided useful information on the spatial and temporal patterns of juvenile Snapper and may provide a useful indicator of year class strength. Furthermore, such data may also help understand the juvenile ecology and demographic and recruitment processes. The purpose here was to summarise the chronology of these studies and to assess these possibilities.

6.3 Results

6.3.1 Differentiating age classes of juvenile Snapper

The historical surveys for juvenile Snapper described below provided indicators of year class strength. To achieve this, it was necessary to differentiate between age classes of juvenile Snapper based on fish size. Whilst it was relatively easy to differentiate between 0+ and 1+ fish, it was less clear for the 1+ and 2+ fish. To resolve this, a comparison of the size distributions of 1+ and 2+ Snapper was done using data extracted from the general Snapper database. Because recruitment studies have focused on NSG, only data from this region were considered here that were collected in February and early March (Feb/March), and April in several years.

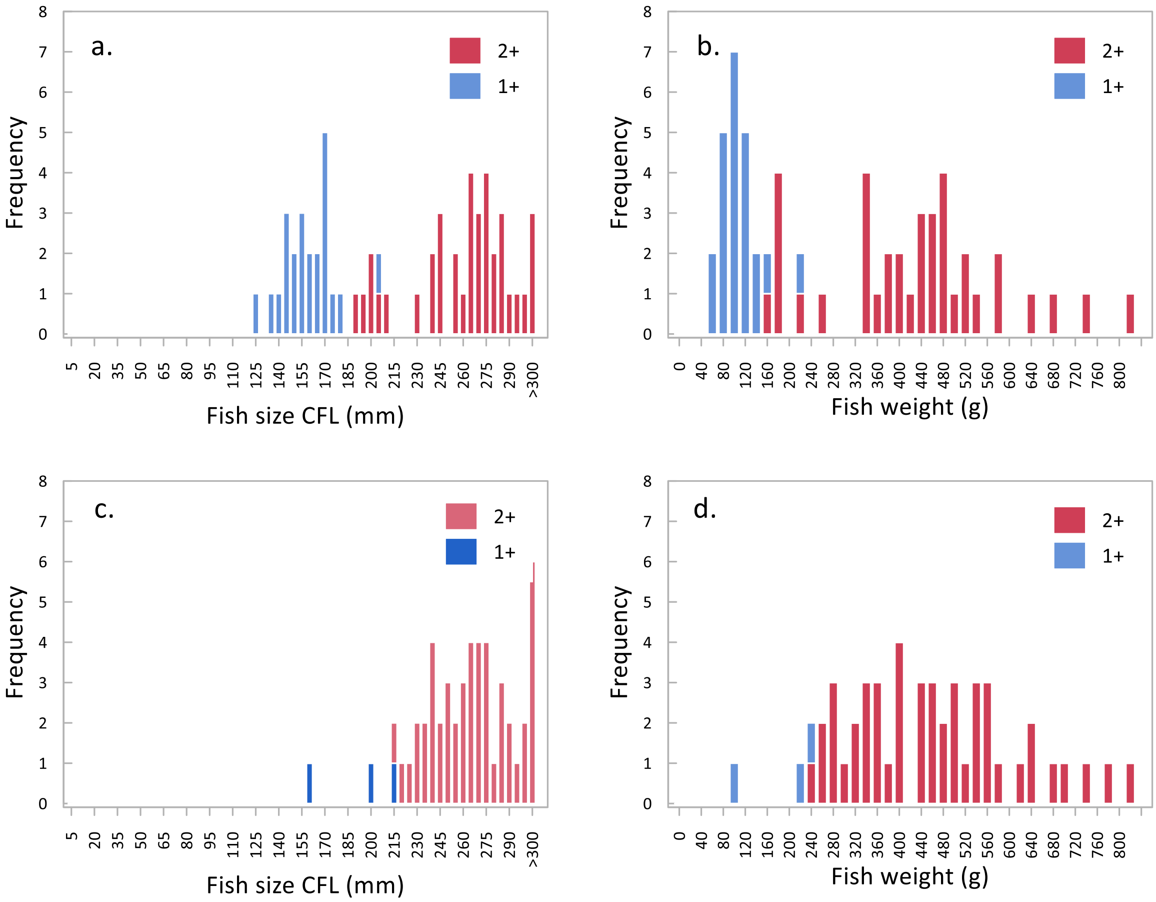


Fig. 6.1. Size and weight frequency distributions for 1+ and 2+ Snapper sampled in Northern Spencer Gulf (from general database). a. sizes of fish collected in February and early March across several years. b. weights of fish collected in February and early March. c. size data for fish collected in April across several years. d. weights of fish collected in April.

For fish collected in February and March in different years there were data on sizes and ages for 60 fish. There was some overlap in the sizes and weights of the 1+ and 2+ fish (Fig. 6.1). The former primarily ranged from 122 to 176 mm CFL and 49 to 150 g although there was one individual of 205 mm CFL and 210 g. The 2+ fish were from 190 to >300 mm CFL, and from 169 to >700 g in weight. All fish that were <185 mm CFL and <150 g were 1+s. For data from April, there were only three 1+ fish. Their sizes were from 158 to 212 mm CFL and weights from 95 to 226 g. Those in the 2+ age class were from 212 to >300 CFL and weight from 222 to 804 g. Although there was some overlap in sizes and weights of fish between age classes, it is likely that most fish that were >215 mm CFL and >240 g were in the 2+ age class.

6.3.2 Trawl-based surveys for juvenile Snapper

January- February 1999

The first sampling for juvenile Snapper in South Australia was done between 31st January and 5th February 1999 (project leader Dr David McGlennon). This exploratory trawling was done at 80 stations throughout NSG that were primarily located between 32°45'S and 33°45'S, with most north of 33°15'S (Appendix Fig. A6.1). Sampling was done with otter trawls that were generally around 10 minutes in duration but ranged from 3 mins 40 secs up to 15 mins 30 secs.

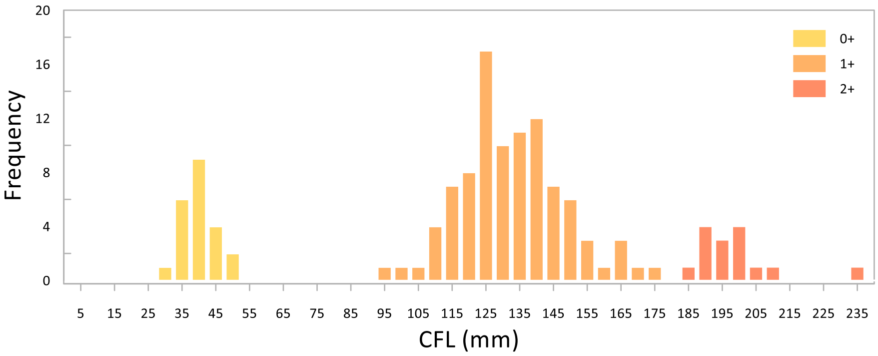


Fig. 6.2. Size distribution of juvenile Snapper captured by otter trawling in NSG in Jan/Feb 1999.

For the 131 juvenile Snapper captured there were three modes in the size distribution (Fig. 6.2). The 22 fish in the size range of 30 to 50 mm CFL were considered recent 0+ recruits. The numerous fish in the second mode, covered the size range of 95 to 175 mm CFL were related to the 1+ age class. The final mode involved fish that were from 185 to 210 mm CFL and one individual of 235 mm CFL that were thought to be in the 2+ age class. The dispersion of individuals in the different age classes differed considerably. The 0+ fish were largely found in one area located between Western Shoal, Musgrave Shoal and the Yarraville Shoals. In comparison, the 1+ and 2+ fish were broadly distributed from Wood Point to north of Point Lowly, including a large group that were caught on an artificial reef in Fitzgerald Bay.

February 2000

The second exploratory sampling of juvenile Snapper in NSG was done from 19th to 23rd February 2000. This sampling was distributed over four zones between the latitudes of 32°45'S to 33°45'S (Appendix A6.1). Two gear types were trialled, i.e., beam trawls and otter trawls. The total sampling effort across both gear types of 118 trawls produced a total of 635 juvenile Snapper that conformed to a unimodal distribution that related to the 1+ age class (Fig. 6.3). No 0+ Snapper were captured.

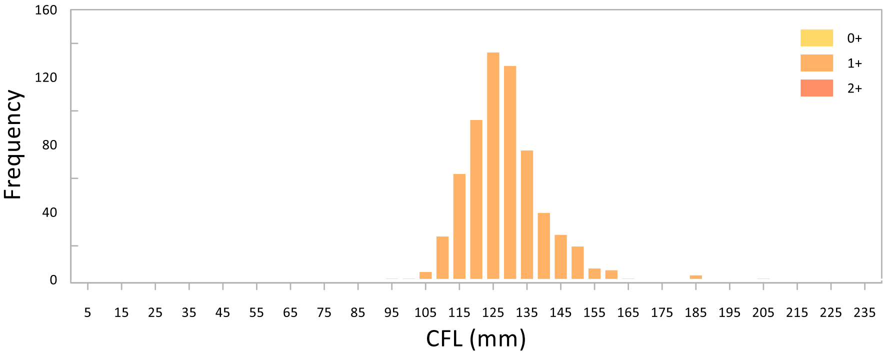


Fig. 6.3. Size distribution of juvenile Snapper captured by otter and beam trawling in NSG in February 2000.

There were 85 beam trawls that produced 96 juvenile Snapper (Table 6.1), at an average of 1.13 Snapper.trawl^{-1}, which were broadly distributed throughout the four zones. In comparison, the 33 otter trawls produced 539 1+ Snapper, at an average rate of 16.3 Snapper.trawl^{-1}. These were also distributed throughout the four zones, with highest catches in the CZ and SZ.

Table 6.1. Details of results from sampling juvenile Snapper in NSG in February 2000 showing number of shots undertaken with the two gear types and the numbers of juvenile Snapper captured.

Zone	No. beam trawls	No. Snapper in beam trawls	No. otter trawls	No. Snapper in otter trawls
FNZ	11	7	11	96
NZ	19	35	7	49
CZ	29	24	9	192
SZ	26	30	6	202
Total	85	96	33	539

Table 6.2. Details of results from sampling juvenile Snapper in NSG in February 2000 showing number of simultaneous shots with the beam trawl and otter trawl and numbers of juvenile Snapper captured.

Zone	No. beam trawls	No. Snapper in beam trawls	No. otter trawls	No. Snapper in otter trawls
FNZ	11	7	11	96
NZ	6	4	6	49
CZ	9	8	9	192
SZ	6	7	6	202
Total	32	26	32	539

This survey also involved a direct comparison between the two gear types. At 32 stations, simultaneous paired tows were done with the beam and otter trawls, which accounted for 64 of the 118 shots. The 32 beam trawls produced 26 juvenile Snapper whilst the otter trawls produced 539 juvenile Snapper (Table 6.2).

April 2000 – 2010

In each year from 2000 to 2010, a survey was undertaken throughout NSG, to provide annual estimates of recruitment rates of the 0+ year class. The sampling methodology and regimes were based on the outcomes of the pilot studies done in 1999 and February 2000. The systematic surveys were done in April of each year to ensure that settlement to the nursery areas for the current reproductive season was completed. In each year, sampling was done from the MRV *Ngerin* using a small purpose-built otter trawl with headline length of 12.9 m, wing height of approximately 2 m and a 12-mm stretched mesh codend (operating at 75% spread efficiency, 9 m swept). Each trawl had a fixed duration of 10 min from when the net hit the bottom until retrieval commenced, with the vessel steaming at 3 – 4 knots. All sampling was done at night to minimize net avoidance by the small Snapper. After each trawl, the catch was searched for juvenile Snapper and any captured were measured for caudal fork length (CFL). The 0+ Snapper were retained frozen at -30°C for future otolith microstructure analysis, whilst 1+ Snapper were measured, weighed but not retained.

For the annual surveys, NSG was divided into five zones, each of 15' in latitude, i.e., Far Northern Zone (FNZ), Northern Zone (NZ), Central Zone (CZ), Southern Zone (SZ) and Far Southern Zone (FSZ) (Fig. 6.4). Within each zone, numerous stations were sampled that were approximately two nautical miles apart. The stations were aligned along transects that were oriented approximately north/south that followed the coastline and passed around shallow shoals (Appendix Fig. A6.2).

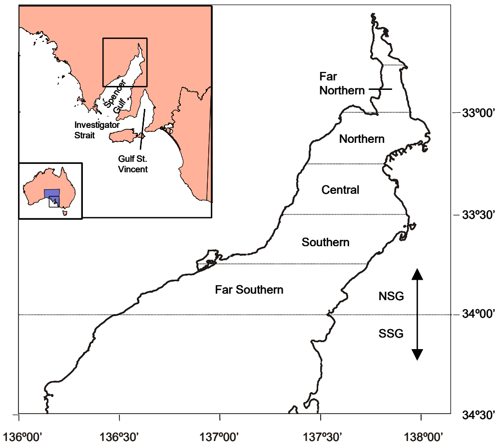


Fig. 6.4. Map of Northern Spencer Gulf showing the five geographic zones in which sampling was done for juvenile Snapper from 2000 onwards.

The total number of trawl stations that were sampled varied amongst years. The highest number was 143 trawls in 2000 (Table 6.3, Appendix Fig. A6.2). This exceptionally high number related to extra trawls that were done in the CZ when we were searching for Giant Australian Cuttlefish (*Sepia apama*), to contribute to Karina Hall's PhD, but the catches of all trawls were processed for juvenile Snapper. Between 2000 and 2005, the numbers of stations were reduced, particularly in the CZ (Table 6.3, Appendix Fig. A6.2). From 2006 onwards, sampling in both the FSZ and SZ was discontinued, as only a single 0+ Snapper had been captured in these zones over the six years from 2000 to 2005. This confined the sampling in subsequent years to the FNZ, NZ and CZ (Appendix Fig. A6.2). In each year the numbers of 0+ and 1+ Snapper were converted to a density per hectare, based on the length of each trawl determined from the start and finish latitudes and longitudes. The area sampled by the trawl was calculated from the equation:

$$A_t = (HxSxD_t/10000);$$

where A_t is the area sampled during trawl 't'; H is the headline length of the trawl net (i.e. 12.9 m); S is the spread factor (i.e. 0.75 from Carrick 1996); D_t is the distance of trawl 't' in metres. Division by 10000 converted the estimated area from square metres to hectares. The density of Snapper per age class for each trawl was calculated as:

$$Dn_a = N_a/A_t;$$

where Dn_a is the density of the age class; N_a is the number of fish sampled in the age class during trawl 't', and A_t is the area of the trawl.

Table 6.3. Summary of results from Snapper juvenile sampling in NSG in annual recruitment surveys in April in each year from 2000 to 2010.

Year	No. stations	No. 0+ Snapper	Stations with 0+ Snapper	No 1+ Snapper	Stations with 1+ Snapper
2000	143	67	19	60	7
2001	122	164	19	0	0
2002	125	8	7	45	13
2003	114	18	7	75	4
2004	110	36	7	91	3
2005	110	2	2	17	6
2006	70	254	16	0	0
2007	69	62	10	9	2
2008	69	3	3	25	3
2009	68	34	7	16	1
2010	69	144	11	4	3
Total	1069	792		342	

0+ Fish

A total of 792 0+ Snapper were captured across the 11 annual surveys, with the numbers highly variable from year-to-year (Table 6.3). To calculate density estimates, the data from the FNZ, NZ and CZ were used as between 2000 and 2005 only a single 0+ Snapper had been captured in the SZ and FSZ. The average annual densities of 0+ Snapper across the three northern zones were highly variable, ranging from 0.03 to 3.9 0+ fish.hectare^{-1} (Fig. 6.5a). Relatively high estimates were recorded in 2001, 2006 and 2010, whilst particularly low estimates were recorded in each of 2002, 2005 and 2008. Generally, the highest densities were recorded in the NZ (Fig. 6.5b). The 0+ Snapper were captured at average depths of 18–19 m in the CZ and NZ and 21-22 m in the FNZ.

The dispersion of the 0+ Snapper was highly consistent from year-to-year with them generally recorded in four areas throughout the three zones. The most significant was on the western side of the gulf around the border of the NZ and CZ (Fig. 6.7). This is a channel that runs from northeast to southwest located south of Western Shoal and west of the Yarraville Shoals. The second area that produced catches of 0+ Snapper was located further north in the NZ, i.e., near False Bay and on the western and eastern sides of the Fairway Bank. Most 0+ fish captured in this area were taken in either 2000 or 2001, with only incidental catches taken from 2002 onwards. The third area that consistently produced 0+ recruits was the FNZ, particularly a few transects located near Backy Point just outside Fitzgerald Bay. The final area was in the southeast of the CZ. The few fish captured here were also primarily taken in 2000 and 2001.

In 2000, substratum analysis was also done at 117 sample stations throughout the five zones in NSG. At each station, after the otter trawl had been completed, a benthic grab sample was taken using a spring-loaded grab deployed from a hydraulic winch located on the starboard side of the vessel. The grab sample was washed into a 500-ml jar and treated with 20 ml of formalin to kill living organisms. On return to the laboratory, each substratum sample was processed for particle size analysis by dividing it by weight into three component fractions using a graded series of sieves that conformed to the Wentworth grade classification of particle sizes (i.e., coarse, particle size > 2mm; sand, 63 µm < particle size <2 mm; and clay/silt, particle size < 63 µm; Holme and McIntyre 1971). Samples were processed wet for splitting into three fractions and to assist with removal of organic material. Samples were oven dried at 80°C for a minimum of 24 h and then weighed to determine their relative contribution to the total sample weight.

The particle size analysis for samples collected in 2000 indicated that the sample area throughout the whole geographic region was dominated by sand except at four places where there was a high clay/silt fraction which gave the substratum a muddy texture (Appendix Fig. A6.3). These four places were: in mid-gulf around the border of the CZ and SZ; at the western border between the CZ and NZ; in the north-western part of the NZ; and in the middle of the FNZ. These were the places that consistently produced the best catches of 0+ fish. As such, the several areas that 0+ Snapper used as nursery areas were characterised by having a muddy texture, the most significant of which was located south of Western Shoal. During 2005 and 2008, i.e. the years of lowest recruitment, there were no recruits in this area.

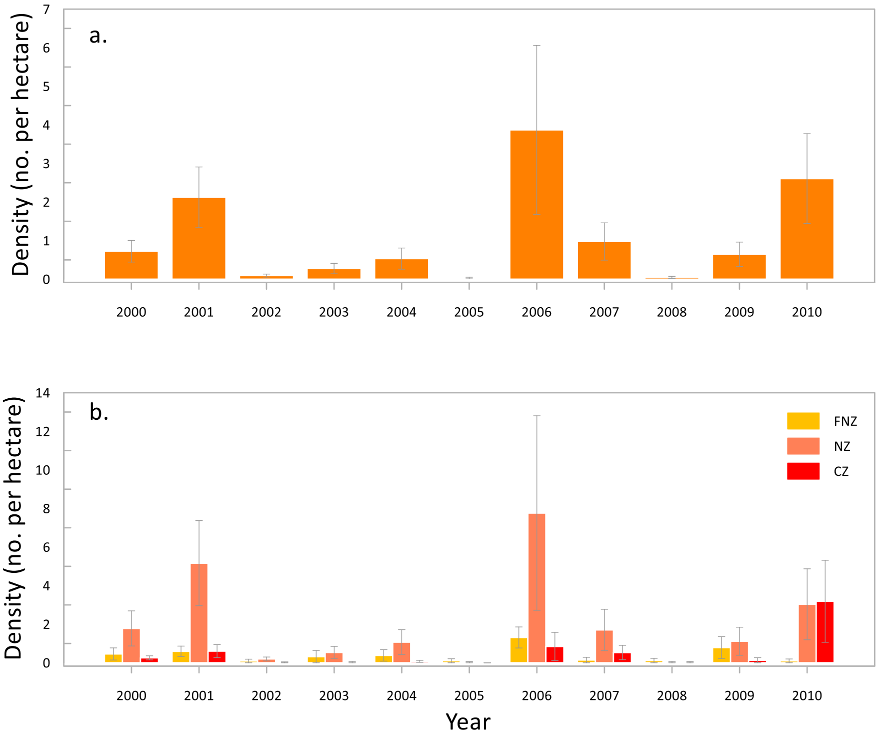


Fig. 6.5. Summary of annual density estimates of 0+ Snapper captured by otter trawls in NSG. a. overall annual density across the FNZ, NZ and CZ. b. average annual density per zone.

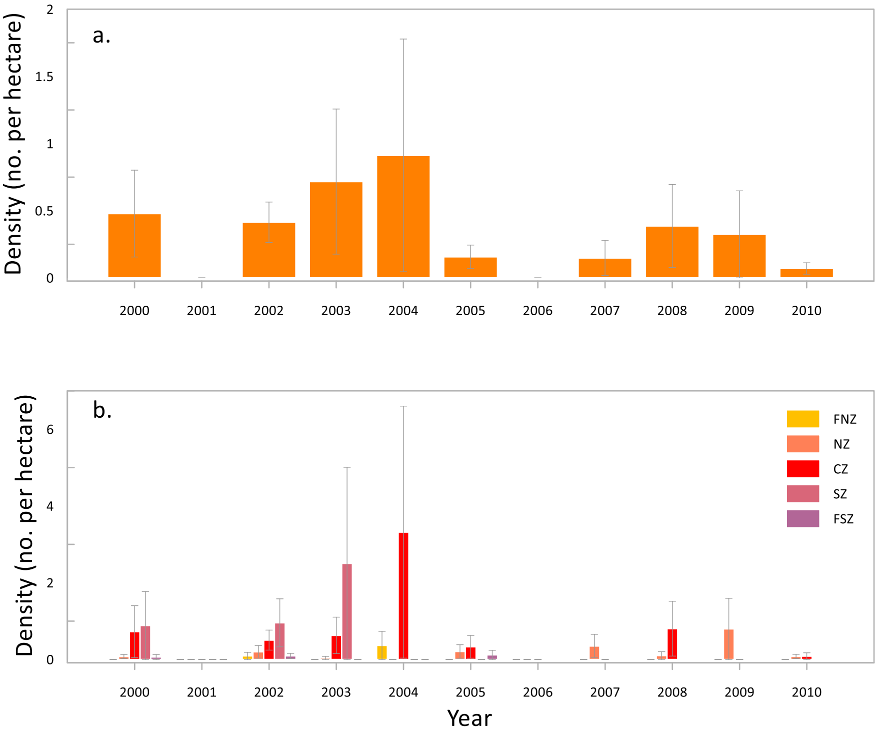


Fig. 6.6. Summary of annual density estimates of 1+ Snapper captured by otter trawls in NSG. a. overall annual density across the FNZ, NZ, CZ, SZ and FSZ. b. average annual density per zone.

1+ Fish

A total of 342 1+ Snapper were captured during the 11 annual trawl surveys (Table 6.3). The numbers were variable amongst years with the highest numbers recorded between 2000 and 2004 and consistently low numbers from 2005 onwards. None were captured in either 2001 or 2006. The average annual densities ranged from 0 to 0.9 1+ Snapper.hectare^{-1}, as estimated across the five zones for 2000 to 2005, and across only three zones for 2006 to 2010 (Fig. 6.6). Higher densities were generally recorded in the former period than the latter. The lower densities in the latter years related, at least partly, to the dispersion patterns of the 1+ fish. In 2000 and 2002, the highest densities were recorded in the SZ (Fig. 6.8). However, as this zone was not sampled from 2006 onwards, there was limited opportunity to catch this age class. From 2000 to 2005, the CZ produced catches of 1+ Snapper, particularly in 2004, but from 2006 onwards their densities were low.

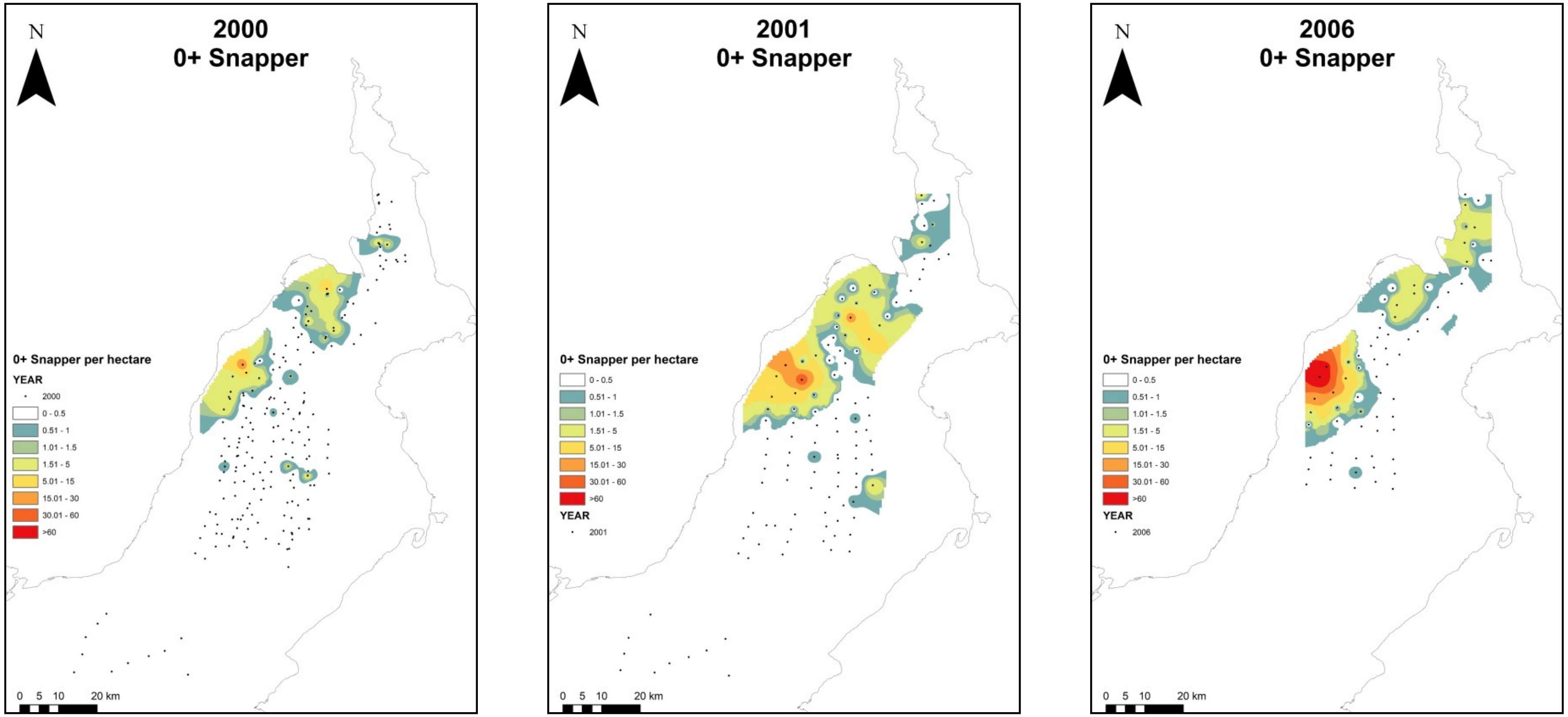


Fig. 6.7. Maps of Northern Spencer Gulf showing the densities of 0+ Snapper caught in the April surveys in 2000, 2001 and 2006.

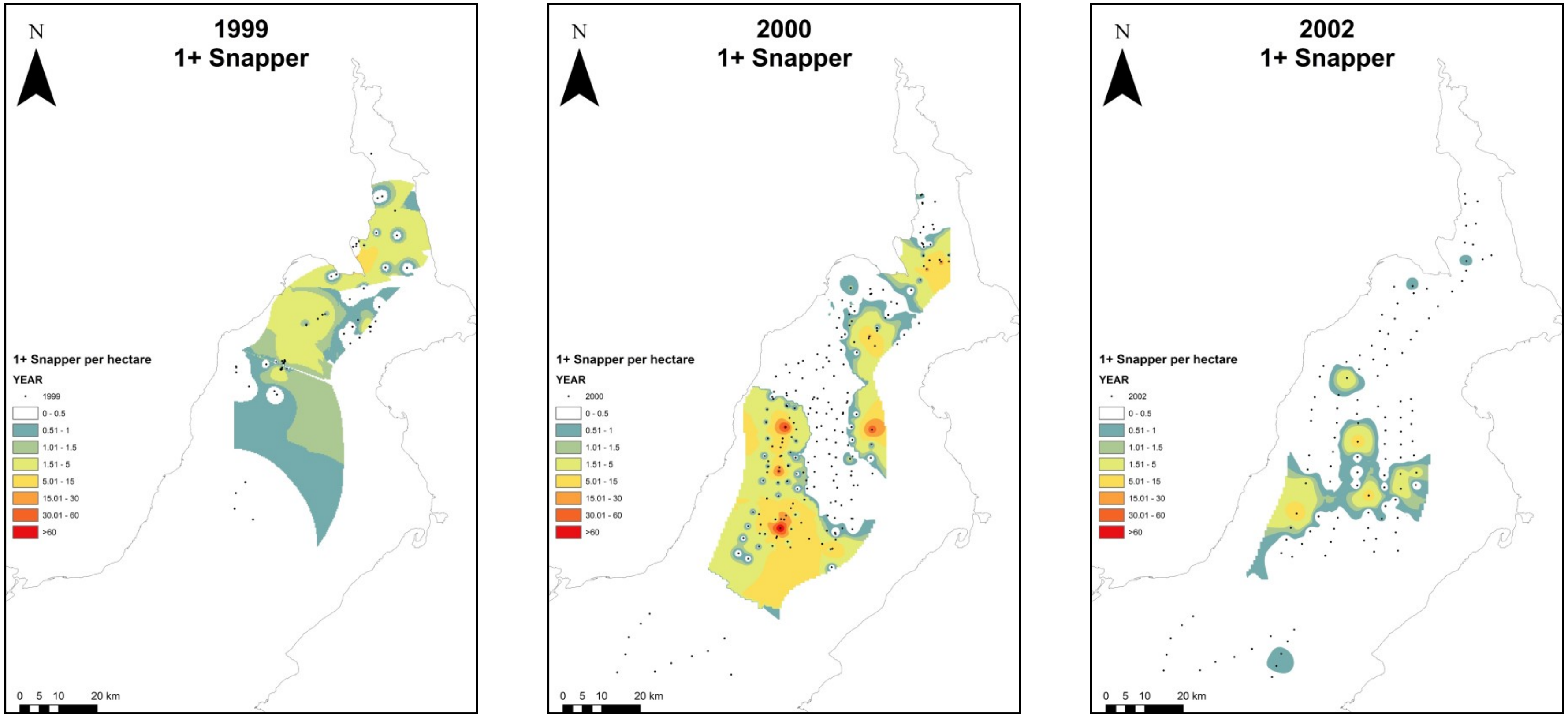


Fig. 6.8. Maps of Northern Spencer Gulf showing the densities of 1+ Snapper caught in February 1999 and the April surveys in 2000, and 2002.

Plumb-staff beam trawl surveys - 2006 and 2007

A second trawl survey for 0+ Snapper was undertaken in NSG as part of the PhD work of Dr Richard Saunders (Saunders 2009). This work used a plumb-staff beam trawl deployed from a trailer boat, a method that had proven effective at sampling 0+ Snapper in Victoria (Hamer and Jenkins 2004). The purpose here was to assess the effectiveness of the otter trawls and to sample in places that were inaccessible to the MRV *Ngerin*. The plumb-staff beam trawl had a 3-m beam, 4 mm^2 knotless mesh in the body of the net and 3 mm^2 mesh in the cod end (Saunders 2009). The net was deployed from a 7-m shark cat and was towed at 1.5 – 2 kn. Each trawl had a fixed duration of 5 minutes from when the net contacted the seabed and when retrieval was initiated. It traversed approximately 300 m of seabed. Sampling was done at night to minimise net avoidance. The sample locations were False Bay, Fitzgerald Bay, Western Shoal and Ward Spit. Two surveys were done in each of 2006 and 2007 with different numbers of shots in the two years (Table 6.4). A third survey was done at Western Shoal in 2006, whilst False Bay was not sampled in 2007.

Table 6.4. Numbers of trawls sampled using the plumb-staff beam trawl net in NSG in 2006 and 2007.

Year - Month	False Bay	Fitzgerald Bay	Ward Spit	Western Shoal	Total no. stations	No. 0+ Snapper
2006 – Feb/March	7	9	9	9	34	8
2006 – April	9	9	9	9	36	24
2006 – May				6	6	22
2007 – Feb		12	12	12	36	10
2007 – March		12	12	12	36	20
Total						

Some 0+ Snapper were captured at the four locations sampled, with numbers higher in 2006 at Ward Spit and Fitzgerald Bay than in 2007 (Table 6.5). The inter-annual comparison was compromised for Western Shoal because different sites and habitats were sampled in the two years. Ward Spit produced the second highest catch rate, suggesting that it may also be another important nursery area. In each year, the fish were generally smaller and younger in the first beam trawl survey than the second (Saunders 2009). Furthermore, the range of ages was also broader in the second survey as it included some small young fish.

Table 6.5. Summary of numbers of 0+ Snapper captured using the plumb-staff beam trawl net in NSG.

Year - Month	False Bay	Fitzgerald Bay	Ward Spit	Western Shoal	No. 0+ Snapper
2006 – Feb/March	3	3	2	0	8
2006 – April	1	6	14	4	25
2006 – May	-	-	-	18	18
2007 – Feb	-	0	1	9	10
2007 – March	-	2	3	15	20
Total	4	11	20	46	81

Gulf St. Vincent juvenile survey

A trawl survey for juvenile Snapper was also done throughout Gulf St. Vincent from 18th to 23rd May 2001. Sample stations were organized in six zones located between the northern gulf and the bays of north-eastern Kangaroo Island (Fig. 6.9), which covered numerous habitat types. The sample methods were the same as those used in the trawl surveys undertaken throughout NSG, i.e., sampling was done from the MRV *Ngerin*, using 10-minute trawls with the otter trawl net. A total of 121 trawls were completed throughout the six zones, with different numbers in the different zones (Table 6.6). The trawl catches included taxa such as Western King Prawns, Strawberry Prawns, Blue Swimmer Crabs as well as a number of different finfish species that included; Skipjack Trevally, Silverbellies, small Leatherjackets, Red Mullet, Blue Sprats, and Slender Bullseyes. Nevertheless, no 0+ or 1+ Snapper were captured at any sample stations.

Table 6.6. Summary of number of trawls completed with otter trawls throughout Gulf St. Vincent in May 2001.

Zone	No. shots
A	19
B	16
C	19
D	23
E	21
F	23
Total	121

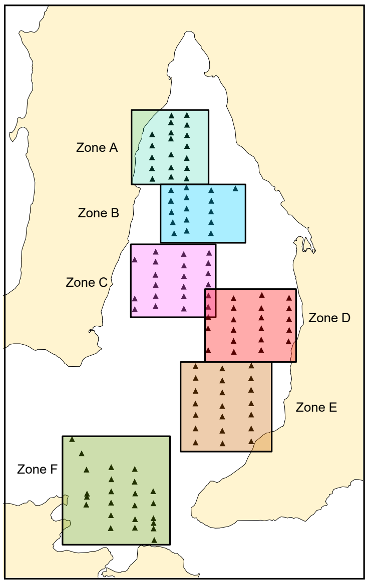


Fig. 6.9. Map of Gulf St. Vincent and the eastern Investigator Strait showing the six zones and the locations of the stations that were successfully sampled in May 2001.

6.3.3 By-catch surveys for Spencer Gulf Prawn Fishery

Surveys during the early 1990s

By-catch surveys for the Spencer Gulf Prawn Fishery that provided information on catches of Snapper were done at various times throughout the 1990s. Some results were presented in the report by Carrick (1996), from which the methods and results presented here were taken. Trawl survey shots were done throughout the five main fishery grounds of Northern, Wallaroo, Gutter, Cowell and Southern located down the length of Spencer Gulf. The surveys were done with 30-minute tows using conventional prawn trawling gear from which by-catch data including the densities and size composition of Snapper were recorded. In both November 1991 and February 1992, relatively large numbers of small Snapper were caught. In November 1991, there were 585 Snapper measured that were from 60 to 120 mm CFL, whilst in February 1992, 449 were in the size range of 90 – 140 mm CFL. A further 562 Snapper caught between April and June 1992, ranged from 80-190 mm CFL. Based on these sizes, most fish from the three time periods were in the 1+ fish relating to the 1991-year class. Such high numbers, compared to those from more recent surveys (see below), indicate that this was a relatively strong year class.

Carrick (1996) indicated that, of the total number of stations sampled, generally few supported juvenile Snapper. In 1991, no Snapper were captured at 92 of 109 stations sampled, whilst multiple Snapper were captured at some stations, with 188 caught at one station at Point Lowly. Such high catch rates at some stations are again consistent with the 1991-year class having been a strong one. In contrast, for the survey in 1996, there were 219 stations sampled, from which no Snapper were captured at 213 stations. At the six stations where Snapper were captured, the highest catch was nine Snapper at a single station. This result suggests that the 1995-year class was relatively weak compared to that which recruited in 1991. This is supported by results from another survey undertaken in February 1996 when 32 prawn trawls were done in deep/shallow pairs in four areas throughout the gulf: Point Lowly to Yarraville; Yarraville to Plank Light; Middle Bank – Wallaroo - Northern Gutter; and in the Southern SG, South Gutter to Corny Point. That survey involved two commercial vessels that trawled conventional gear for 30 – 40 minutes at each station. Only 14 Snapper were captured, primarily in the northern region near Whyalla.

Several significant conclusions were drawn from this early work on the by-catch of the Spencer Gulf Prawn Fishery (Carrick 1996). First, Snapper were caught infrequently during prawn trawling in SG, but occasionally in large numbers, reflecting substantial spatial and inter-annual variation in capture rates. He concluded, based on the sizes of the Snapper, that they were less than one year old and that the variation in numbers reflected inter-annual variation in recruitment rates. We now know that most Snapper captured in prawn trawls come from a single year class, but their age class i.e., 0+

or 1+ depends on the time of year when captured (i.e., fish captured in November and then the following February are from the same year class, but the former are 0+ and the latter 1+ because of the assigned birth date of 1st January) (Chapter 9). Carrick (1996) compared the sizes of Snapper captured in prawn nets with those taken with other gears and the commercial Marine Scalefish Fishery, concluding that larger Snapper can avoid capture in prawn nets.

Surveys during the latter 1990s and early 2000s

A second report on by-catch from the Spencer Gulf Prawn Fishery provided information on catches of Snapper from six annual surveys (Dixon et al. 2005). From 1994, by-catch data were collected opportunistically during prawn surveys that were done using commercial prawn trawlers throughout eight regions of the gulf: North; Middlebank/ Shoalwater; Wallaroo; Cowell; Main Gutter; Wardang; West Gutter; and South Gutter. Several assumptions were made by Dixon et al. (2005), for the data analyses: data were collected from a single net only; each trawl was 30 minutes in duration; abundance data (count and weight) included all individuals captured in the trawl.

Table 6.7. Details of timing and number of prawn survey shots for which by-catch data were processed for the Spencer Gulf Prawn Fishery, as considered by Dixon et al. (2005).

Date of survey	No. trawl shots	No. Snapper	Size range (mm TL)
Nov 1997	52	?	
Feb 1998	129	543	90 -180
Nov 1999	61	318	50-140
Feb 2000	152	495	70-180
Nov 2001	104	?	
Nov 2002	140	?	

Between 1997 and November 2002, the numbers of stations for which data on by-catch from prawn trawls were collected varied amongst the six surveys (Table 6.7). Size structures for the captured Snapper were presented for each of February 1998, November 1999, and February 2000. In each case, they were relatively small (Table 6.7), and primarily related to the 1+ age class (Section 6.3.1). As such, the 543 Snapper captured and measured in February 1998 related to the 1997-year class, whilst the high numbers in November 1999 and February 2000 related to the 1999-year class.

The spatial data from the surveys were presented in terms of the relative biomass of Snapper captured at the different stations (Dixon et al. 2005). In February 1998, catches of Snapper were broadly dispersed throughout the North Region, although were generally <2.0 kg at most stations (Appendix Fig. A6.4). The catches were also relatively consistent throughout the Main Gutter. The broad spatial dispersion and the large number of 1+ Snapper measured suggest that the 1997-year class was relatively strong. In February 2000, the numbers of Snapper captured were even higher and more widely dispersed than in 1998. Nearly every station throughout the North, Middlebank/Shoalwater and Wallaroo Regions supported Snapper and the catches at numerous stations were >2.0 kg.shot^{-1}, suggesting that the 1999-year class of recruits was even stronger than that in 1997. This year class was also apparent as 0+ fish in November 1999 when, at several stations sampled in the North, catches of up to 2.0 kg were sampled. The surveys undertaken in each of November 2001 and 2002, were geographically extensive, but only incidental catches of 0+ snapper were made in both years. These results do not suggest that either the 2001 or 2002-year classes were particularly strong.

Whilst it appears that the catches of Snapper as by-catch in prawn trawls in the Spencer Gulf Prawn Fishery may be useful at providing an indication of year class strength, there is one inconsistency in the results presented that needs some consideration, i.e., between the results obtained in November 1997 and those obtained in February 1998 (Appendix Fig. A6.4). Since prawn surveys primarily sample a single year class (i.e., either 0+ or 1+ depending on time of year), these two surveys sampled the 1997-year class. The first provided only incidental catches of Snapper, whereas for the second, the catches were high and dispersed throughout the North Region. The ambivalence here may relate to the relatively few stations that were sampled in November 1997 and their locations. Those stations that had produced catches of Snapper in November 1999 had not been sampled in November 1997, thus minimising the opportunity of sampling 0+ Snapper in the former year.

Surveys in February 2007 and February 2013

In February 2007, a comprehensive study of the by-catch of the Spencer Gulf Prawn Fishery was undertaken (Currie et al. 2009). A total of 120 stations were sampled by eight commercial trawlers over four consecutive nights (16-19 February 2007). The sites were distributed throughout the gulf southward from Point Lowly to the gulf entrance and were stratified to reflect the range of depths (>10 m) that were historically fished and to maximise the variety of sediment types (mud, sand, gravel, rhodolith) and sea-scapes (banks, gutters, bays) sampled (Appendix Fig. A6.5). In February 2013, a similar study was done to re-assess the spatial distribution of by-catch species in relation to trawling activity by the Spencer Gulf Prawn Fishery (Burnell et al 2013). By sampling in both 2007 and 2013 allowed the first fishery-wide comparison of by-catch from the Spencer Gulf Prawn Fishery. In 2013, trawls for by-catch re-assessment were undertaken at 65 stations in Spencer Gulf compared to the 120 considered in 2007. Some stations in areas of low trawl intensity were removed from the design and some sites were not sampled due to difficulty with the trawling gear.

In both 2007 and 2013, trawls of approximately 30-min duration were done using standard double-rig prawn gear (Table 6.8). One level fish bin of unsorted catch was retained and frozen from a single trawl net at each site. The remaining catch was weighed before being processed by the crew with commercial-sized prawns and by-product removed and the by-catch discarded overboard. In the lab, the contents of the frozen samples were thawed and sorted into their component taxa and quantified. The captured Snapper were counted, measured and weighed.

From the survey in February 2007, a total of 85 Snapper were captured across the 120 stations. Based on their sizes, 61 were in the 1+ age class. When multiplied up to the total catches from the various stations, this led to an estimate of 157 1+ Snapper captured across the 120 stations (Table 6.8). Their distribution was largely throughout the northern gulf (Appendix Fig. A6.5). The highest numbers were detected in the NZ and at one station near Point Lowly in the FNZ. Snapper were also caught at numerous stations throughout the CZ and SZ. Whilst a high number were sampled at Station 58C, located in the south-eastern corner of the CZ, the numbers generally declined southward through the CZ and SZ. There were also a few Snapper captured at two stations in the FSZ. Furthermore, despite considerable sampling effort, only a few 1+ Snapper were captured in the southern gulf, all of which were from the eastern side of the gulf.

In 2013, only two Snapper were captured across the 65 stations. One was 146 mm CFL, falling in the size range for 1+ Snapper. It was sampled in the northern part of the SZ (Appendix Fig. A6.5). The other Snapper was 199 mm CFL, for which the age class was ambiguous. It was collected from the southern end of the CZ. As there were two bins of by-catch collected at this station, the catch of Snapper for this station multiplied up to two fish.

At least part of the lower catches of 1+ Snapper between February 2013 compared to 2007 can be attributed to the fewer stations that were sampled. Nevertheless, many stations sampled in the latter year had produced catches of Snapper in 2007. So, the lower catch rates and spatial dispersion of Snapper between these years, suggests that there was also a considerable difference in recruitment rates between the two years, with the 2006-year class considerably stronger than the 2012-year class.

By-catch surveys 2019 to 2021

Recently, a new protocol for monitoring by-catch in the Spencer Gulf Prawn Fishery has been established based on Marine Stewardship Council criteria. Information is captured on catches of 20 by-catch species that were selected based on conforming to one of the following criteria: they comprised >2% of the total catch; had established reference points for management; or were endangered, threatened, or protected species. Snapper was included as a monitored by-catch species as it is an important fishery species for which there are established reference points.

The new sampling protocol involves collecting by-catch data during stock assessment prawn trawl surveys that are done throughout the gulf, with different sub-sets of species considered on alternating shots. Data for the by-product species of Southern Calamary and Balmain Bugs are collected on every shot. For 'crab' shots, data are also collected for Blue Swimmer Crabs. For 'fish' shots, data are collected on finfish species. For the 'none' shots, data are only collected on the by-product species, but not for crabs or finfish. This sampling design was developed so that data collection would be manageable by scientific observers onboard the vessels, given the potential for capture of large numbers of some species, and the requirement that by-catch be processed onboard in the limited time between shots. This new protocol was field-tested in October 2019. The trial involved two boats and observers out of the nine boats involved in the survey. Of the 172 stations sampled throughout the gulf, there were 14 'fish' shots, which were primarily done in NSG (i.e., throughout the NZ, CZ, and SZ), near where juvenile Snapper had been captured in previous surveys (Appendix A6.6). Nevertheless, no Snapper were captured at any of the 14 stations.

Table 6.8. Summary of by-catch surveys done for the Spencer Gulf Prawn Fishery throughout the 2000s.

Year - survey	Type of survey	Total no. stations	Number sampled for Snapper	Number of 1+ Snapper	Recruitment year class
February 2007	Whole	120	120	157	2006
February 2013	Whole	65	65	1	2012
October 2019	Partial	172	14	0	2019
March 2020	Partial	190	47	0	2019
October 2020	Partial	162	59	7	2020
March 2021	Partial	143	50	522	2020

In March 2020, all nine boats involved in the stock assessment survey participated in the by-catch sampling. A total of 190 stations were sampled throughout the gulf of which 47 were 'fish' shots (Table 6.8). In this survey, by-catch was not considered at the ~40 stations located in the northern gulf, which are reserved for measuring prawns to obtain an annual recruitment index (Appendix A6.6). So, the 'fish' stations sampled were distributed from around Yarraville Shoals to as far south as Corny Point. This meant that the FNZ and NZ were not sampled with 'fish' shots, but the CZ, SZ and FSZ were each sampled with numerous shots, as well as several stations near Corny Point. Across the 47 'fish' stations, there was only a single Snapper captured, i.e., a 1 kg fish from near Corny Point that was excluded as a 1+ Snapper.

From the prawn stock assessment surveys done in October 2019 and March 2020, there were 61 stations sampled for 'fish', many of which had produced catches of 0+ and/or 1+ Snapper in previous years. The zero catches of 0+ and 1+ Snapper across the two surveys (Table 6.8), suggest that the 0+ year class in 2019 was likely to have been a poor one.

In October 2020, another prawn stock assessment survey was carried out during which by-catch was considered. A total of 162 stations were sampled throughout the gulf, which included 59 'fish' shots. Seven Snapper were captured (Table 6.8). A fish that weighed 100 g and a further six

Snapper with a combined weight of 100 g were captured in the NZ in the north-western gulf (Appendix Fig. A6.7). They were likely to have been 0+ fish that had recruited earlier in 2020.

In March 2021, by-catch was considered during the prawn stock assessment survey. A total of 143 stations were sampled, of which 50 ‘fish’ shots were distributed throughout the gulf from the CZ southward. They produced an estimated 522 Snapper (Table 6.8). For these, there were no measurements of size, as for each station only the total count and weight, (or weight of a sub-sample), which allowed calculation of the average weight of the Snapper from each transect. The average weights of the Snapper caught ranged from 48 to 240 g.shot^{-1}. These were all relatively small and conformed to the weight range of the 1+ Snapper. As such, it is assumed that all Snapper captured during this survey were in the 1+ age class. They were taken at eight of the 50 transects located in the regions of Wallaroo, Middlebank, Stones and Plank (Appendix Fig. A6.7). There were several transects that had relatively high counts of 1+ Snapper. In fact, to date, the count of 385 Snapper at Middlebank N22 was the highest ever recorded from all by-catch and 0+ surveys. There were two stations at Stones that produced counts of 80 and 12 Snapper, whilst 16 were recorded at Plank. These stations are all in the CZ. Such catches in March 2021 suggest a relatively strong 2020 recruitment year class.

6.4 Discussion

6.4.1 Trawl-based surveys for juvenile Snapper

The first benthic trawling for juvenile Snapper in South Australia was done in NSG in February 1999. This and the following sampling trip in February 2000 were largely exploratory, focussed on assessing the capability of trawling gear and the dispersion of juvenile Snapper. Based on these experiences, in April 2000 a systematic sampling regime was initiated to provide broad spatial coverage throughout the northern part of the gulf (Fowler and Jennings 2003, Fowler et al. 2010). Systematic sampling was then undertaken in April of each year until 2010. These surveys were done with an otter trawl from the MRV *Ngerin*, which precluded the possibility of sampling in shallow nearshore waters. Throughout these 11 years, the spatial coverage of the sampling regime was gradually contracted northwards based on the emerging understanding of the dispersion of the 0+ Snapper. After an interim period of eleven years, otter trawl sampling for 0+ Snapper was trialled again in 2021, as part of FRDC project 2019/046 (Rogers et al. 2021).

0+ fish

In February 2000, a comparison between beam and otter trawls indicated that the latter provided substantially higher catches for the same sampling time, as more seafloor area was sampled. As such, otter trawling was used in each April survey from 2000 to 2010, producing catches of both 0+ and 1+ Snapper. For the 0+ age class the catches and catch rates were highly variable amongst years. Catch rates of <1.0 Snapper.hectare^{-1} were recorded in each year of 2000, 2002-2005 and 2007-2009, whilst the catches of 0+ fish in each of 2001, 2006 and 2010 were >2.0 0+.hectare^{-1}. There were two orders of magnitude difference in the catch rates between the lowest and highest years. Such temporal variability has proven to be characteristic of Snapper recruitment at numerous places in southern Australia (Hamer and Jenkins 2004, Hamer and Conron 2016) and elsewhere (Azeta et al. 1980, Francis 1993, 1995).

The densities of 0+ Snapper in NSG from the otter trawls were generally very low compared with elsewhere. In Port Phillip Bay (PPB), 0+ Snapper have been sampled annually since 2000, providing an annual recruitment index (Hamer and Jenkins 2004, Hamer and Conron 2016). Annual estimates of average density across numerous sites around PPB has ranged from approximately zero to 150 fish.hectare^{-1} (recalculated from Hamer and Conron 2016). The latter is approximately 40 times higher than the highest density estimate of 3.9 0+ Snapper recorded in NSG in 2006. Between 2000 and 2003, the estimates of recruitment rates in Corner Inlet and Gippsland Lakes in Victoria were also generally higher than those for NSG (Hamer and Jenkins 2004). Densities of 0+

Snapper in three estuaries in New South Wales (recalculated from Ferrell and Sumpton 1998), were also approximately an order of magnitude higher than those recorded in NSG.

Despite the inter-annual variability in catch rates of 0+ Snapper in NSG, there was considerable spatial consistency in where they were captured. From 2000 to 2005, only a single 0+ individual was recorded across both the SZ and the FSZ. So, sampling in these zones was discontinued from 2006 onwards. For the northern zones, the highest catches were consistently recorded in the NZ with fewer in the FNZ and the CZ. However, the densities were not consistent within these zones. Rather, there were four areas where the 0+ Snapper were captured. These areas were ~18-19 m in depth and supported areas of muddy substratum, as distinct from coarser sand or gravel that were more typical of the benthic substratum throughout NSG. The plumb-staff beam trawl work in 2006 and 2007 identified a further area, i.e. Ward Spit where relatively high densities of 0+ Snapper occurred (Saunders 2009).

1+ fish

The otter trawl sampling also provided catches of 1+ Snapper. There were several important observations for this age class of fish with respect to the temporal aspects of the catches and the spatial aspects of their dispersion. Firstly, the catch rates were variable amongst years, with the densities from the April surveys ranging from zero to 0.9 Snapper.hectare^{-1}. Furthermore, the highest catches were recorded in February 1999 and 2000, compared with sampling in April in any year. The highest catch was in February 2000 when 539 1+ Snapper were recorded from 33 otter trawl shots. The second observation with respect to the 1+ fish is that their dispersion differed from that of the 0+ fish. From 2000 to 2004, their highest catches were recorded in the CZ and SZ, as distinct from the NZ for the 0+ fish. Furthermore, the 1+ fish tended to be highly aggregated, i.e., relatively high catches were made at some stations. These observations suggest that the 1+ fish had moved out of the nursery areas used by the 0+ fish, and had aggregated, perhaps around small areas of reef or structure.

The extent to which our estimates of catch rates of 1+ Snapper from 1999 to 2010 can be interpreted in terms of year class strength is limited by the change that was made to the sampling regime in 2006. The highest numbers of 1+ fish were recorded between 2000 and 2004, particularly in the SZ. So, the lower numbers from 2006 to 2010 might reflect that this zone was not sampled in those years. This spatially-condensed sampling that was done in these latter years is likely to have restricted opportunity to fully document the patterns of distribution and abundance of the 1+ fish.

6.4.2 By-catch surveys for Spencer Gulf Prawn Fishery

Since the 1990s, there has been a focus on documenting the by-catch from prawn trawling by the Spencer Gulf Prawn Fishery. This has generally been done from stock assessment surveys or by-catch surveys, both of which have generally involved trawlers using conventional double-rigged prawn trawling gear and 30-minute shots. Also, the surveyed region has generally been geographically extensive, i.e., from Point Lowly in the north to Corny Point in the south. As such, by-catch surveys have provided considerably greater spatial coverage than the otter trawl surveys.

The by-catch from prawn trawling in Spencer Gulf includes juvenile Snapper. Based on our understanding of the sizes of Snapper in the younger age classes, and the sizes of the captured Snapper presented in various reports (Carrick 1996, Dixon et al. 2005, Currie et al. 2007, Burnell et al. 2013), the by-catch was dominated by juveniles in a single year class. Few larger, older Snapper were evident in prawn trawls, suggesting that such fish can avoid the nets (Carrick 1996). The information on catches of Snapper in prawn by-catch surveys was assessed for its usefulness as an indicator of year class strength. It was determined that the age class to which the captured Snapper belonged depended on the time of year of the sampling. If done in October, the captured Snapper primarily belonged to the 0+ age class that had recruited earlier in the same year. If sampled in February, March, or April they belonged to the 1+ age class, having recruited during the summer prior to the one that had just finished. So, prawn trawl by-catch considered in October and the following March related to the same year class of Snapper.

The results of the first studies on by-catch in the Spencer Gulf Prawn Fishery were summarised by Carrick (1996). From surveys in November 1991 and February 1992, he reported relatively high numbers of Snapper in the size range of 70-140 mm CFL, which related to the 1991-year class. In comparison, from the survey in February 1996, there were relatively few 1+ Snapper captured. Such comparative data suggest that the 1991-year class was considerably stronger than the 1995-year class. Carrick (1996) suggested that such differences in catch rates of Snapper amongst years reflected inter-annual variation in recruitment rates. He also observed that the numbers of stations that supported juvenile Snapper were generally low, but multiple Snapper could be caught at a single station.

Dixon et al. (2005) provided the second analysis of by-catch from the Spencer Gulf Prawn Fishery, summarising results from six different surveys that were done either in November or February in different years. They provided useful indicators of the 1997 and 1999-year classes, as well as some valuable insight about sampling at different times of the year. There was also an important difference between the observations of Dixon et al. (2005) and Carrick (1996), with respect to numbers of stations on which juvenile Snapper were detected. In February 1998, juvenile Snapper were captured at most stations sampled through the NZ and the CZ. They were even more broadly dispersed in February 2000, being captured at most stations throughout the NZ, CZ, SZ and even the FSZ. Such high catch rates and broad spatial dispersion of the 1+ Snapper are consistent with the 1997 and 1999-year classes in NSG being relatively strong. Nevertheless, the catch rates of Snapper in November 1997 and 1999 were not particularly high, suggesting that year class strength might be best indicated by sampling in February rather than in the preceding November.

The by-catch surveys that were undertaken in February 2007 and 2013 (Currie et al. 2007, Burnell et al. 2013), provided measures of the relative strengths of the 2006- and 2012-year classes. There was considerable disparity in the catch rates of the 1+ Snapper between these surveys. The estimated total of 157 1+ Snapper captured from 120 stations throughout the gulf in 2007 was relatively high. They were distributed broadly throughout the NZ, CZ, SZ and the FSZ and the southern gulf near Corny Point. In comparison, at 65 stations sampled in February 2013, only three Snapper were captured. This comparison suggests that the 2006-year class of Snapper was considerably stronger than the relatively weak 2012-year class.

During 2019, a new sampling regime for documenting the by-catch in the Spencer Gulf Prawn Fishery was developed. The intention for the future is that this regime be applied during stock assessment surveys in March and October each year. This new sampling regime was first trialled in October 2019, when finfish by-catch was documented at 14 of 172 trawl stations sampled throughout the gulf. Then, in March 2020, the sampling regime was fully applied, with finfish by-catch documented at 47 out of 190 stations. Across the total of 61 ‘fish’ stations that were considered across both surveys, no 0+ or 1+ Snapper were captured. This strongly indicates that the recruitment year class for Snapper in 2019 in Spencer Gulf was poor. In comparison, a total of 109 ‘fish’ stations that were sampled in October 2020 and March 2021, provided an estimated total of 522 Snapper from the 2020-year class. Although 385 of these were caught at a single station, the remainder were broadly dispersed. This high number of 1+ Snapper, and their broad dispersion suggests that the 2020-year class was a relatively strong one.

It is apparent that by-catch surveys undertaken by the Spencer Gulf Prawn Fishery provide useful information on the year class strength of Snapper. The by-catch surveys done through the 1990s and 2000 identified that the 1991, 1997, 1999, 2006 and 2020-year class classes were relatively strong, whilst the 1995, 2012 and 2019-year classes were relatively weak. These are clearly qualitative assessments. At this stage it is difficult to scale the relative strengths of the different year classes against each other as in each year different methods for quantifying the by-catch were used. Nevertheless, there are some observations that provide confidence in the qualitative assessments. The proposition that the high catches of Snapper from the 1991, 1997 and 1999-year classes are indicative of strong year classes is consistent with the identification of these as strong ones, based on the analysis of population age structures (Chapter 9, Fowler and McGlennon 2011, Fowler et al. 2016, 2020). Furthermore, that the 2006-year class was relatively strong is corroborated by the results of the otter trawling, for which that year produced the highest number and density estimate of the 0+ Snapper. The standardisation of the sampling methodology for by-catch surveys by the Spencer Gulf Prawn Fishery in 2019 provides an opportunity to obtain consistent, comparable, quantitative estimates of the year class strength for Snapper.

6.4.3 Habitat associations for juvenile Snapper

The by-catch surveys provided some compelling results with respect to the spatial aspects of Snapper recruitment in Spencer Gulf. These results are consistent with the finer-scale results from the otter trawls for juvenile Snapper. Most 0+ and 1+ Snapper were captured in the northern part of the gulf. Relatively few juveniles have been captured south of 33°45’S, i.e., the line across the gulf from Franklin Harbor to Tickera. This suggests that NSG is the primary source of recruits for the whole gulf and possibly the whole SG/WC Stock (Chapter 10, Fowler et al. 2017). In the by-catch surveys in October/November, 0+ Snapper were generally located on the western side of the NZ and CZ in the northern gulf. Nevertheless, by February of the following year, the 1+ age class were captured more broadly across the centre of the northern gulf, down through the SZ and across to the eastern side of the FSZ near Wallaroo. The few juvenile Snapper captured further south tended to be on the eastern side of the gulf with only incidental captures of juvenile Snapper reported from the western gulf south of Franklin Harbor.

It is apparent from numerous studies that have sampled juvenile Snapper in different jurisdictions in Australia, New Zealand and elsewhere that such fish use nursery areas that are located in relatively protected coastal waters of estuaries, bays and harbours. Within these coastal environments, they can occupy a diversity of habitats from relatively deep areas of bare sediment through to shallow seagrass beds. At particular places, the juveniles might be distributed across a range of habitats, amongst which the abundances reflect a gradation in habitat preference. However, these habitat preferences are not consistent amongst different places.

For NSG, throughout which the substratum is generally dominated by sand or coarser substratum, the 0+ Snapper were strongly associated with relatively small areas characterised by muddy substratum (Fowler and Jennings 2003). This apparent habitat preference for muddy areas was also the case in Port Phillip Bay, Victoria (Hamer and Jenkins 2004), which is the major nursery area for the Western Victorian Stock (Hamer et al. 2011). Similarly, in Kawau Bay, Hauraki Gulf, New Zealand, the 0+ and 1+ Snapper were most abundant in areas characterised by muddy substrate rather than areas where the sea bottom had higher amounts of sand and shell (Francis 1995). In Shijiki Bay, northern Japan, the abundances of the 0+ juveniles of the Red Sea Bream

(*Pagrus major*) reflected a preference gradation. The highest abundances were recorded in areas characterised by 'fine sand' (probably mud – from Francis 1995), located well towards the inner part of the bay (Tanaka 1985). They next preferred areas with soft substrate and beds of *Zostera* sp. or the alga *Sargassum* sp. Then, the next preference was for areas of coarser sediments, whilst few Snapper occurred in sandy areas near the mouth of Shijiki Bay. This order of habitat preference, as reflected in the abundances of the juvenile fish, was also apparent in their condition, their fat content and the weight of stomach contents suggesting that the habitat preference reflected the variation in quantity and quality of food available. For NSG, there was spatial variation in the diet of the 0+ Snapper. For those captured in the preferred area near Western Shoal, the diet was dominated by polychaete worms compared to those from elsewhere for which the diet was dominated by teleost fishes and crustaceans. As such, the success of the former as a nursery area might relate to the prey fauna available (Saunders et al. 2012).

There was an important observation from Carrick (1996) with respect to the habitat preferences of juvenile Snapper in NSG. In May 1992, he undertook an experimental trawl survey which compared the catch rates amongst three different habitats: artificial reef complex (car bodies); the main trawl grounds (channel); and a high bank area (Carrick 1996). The densities of trawled Snapper were significantly higher around the artificial reef complex (114 fish.hr^{-1}) compared to the higher banks (30 fish.hr^{-1}), and the trawl grounds (1 fish.hr^{-1}). Given the timing of this study, the captured fish were likely to have been 1+ fish from the strong 1991-year class. The results are consistent with the fish of this age class having aggregated around artificial reef. For juvenile Snapper in nursery areas in New Zealand, the patterns of distribution and abundance of the 1+ age class were influenced by micro-habitat features in the soft sediments, such as depressions, burrows, shells, boulders, cobbles, and sand waves. Such features were thought to provide refugia from predation, rather than influencing the availability of food (Thrush et al. 2002).

In the studies described above where juvenile Snapper were strongly associated with muddy, soft-sediment substrata, the water depths were relatively deep, i.e., >10 m. In contrast, some studies have shown juvenile Snapper to be more abundant in shallow water. This is the case in Moreton Bay in southeast Queensland, where higher numbers of juvenile Snapper occur in the southern bay waters in 0-10 m depth (Sumpton and Jackson 2005, Bessell-Brown et. al 2020). Catch rates in deeper areas of Moreton Bay were an order of magnitude lower than in areas of <5 m depth. In the shallow waters, juvenile Snapper were associated with several types of substrata; sand, mud, rubble, soft coral/algal beds. In the numerous nursery areas around the New Zealand coastline, the post-settlement Snapper appear to aggregate around biogenic structures (Parsons et al. 2014). For example, abundances in shallow seagrass beds were up to 50 times greater than in adjacent areas of bare sand or mud. The differences in abundance reflect the availability of prey for the juvenile fish (Sim-Smith et al. (2012).

Across the distribution of Snapper, the juvenile fish have occupied a diversity of habitats in nearshore, enclosed coastal waters. These habitats vary with respect to the types of sea bottom, sediment, biogenic and physical structural components and water depth. It has been speculated that this versatility has contributed to the success of this species in occupying such a broad distribution throughout the temperate and sub-tropical waters of Australia, New Zealand and elsewhere (Sumpton and Jackson 2005).

6.5 References

Azeta, M., Ikemoto, R., Azuma, M. (1980). Distribution and growth of demersal 0-age red sea bream, *Pagrus major*, in Shijiki Bay. Bulletin of the Seikai Regional Fisheries Research Laboratory 54: 259-278.

Bessell-Brown, P., Prosser, A., Garland, A. (2020). Pre-recruit abundance indices for Eastern King Prawn, Blue Swimmer Crab and Snapper in south eastern Queensland. Report to Fisheries Queensland, Department of Agriculture and Fisheries. 21 pp.

Burnell, O.W., Barrett, S.L., Hooper, G.E., Beckmann, C.L., Sorokin, S.J., Noell, C.J. (2015). Spatial and temporal reassessment of by-catch in the Spencer Gulf Prawn Fishery. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2015/000414-1. SARDI Research Series No. 860. 128 pp.

Carrick, N. (1997). A preliminary assessment of the by-catch from the Spencer Gulf Prawn Fishery. South Australian Fisheries Assessment Series 97/02. 57 pp.

Cartwright, I., McPhail, J., Knuckey, I., Smith, T., Rayns, N., Steer, M. (2020). National Snapper Workshop – Rebuilding our iconic Snapper stocks. Final report to FRDC (Project No. 2019/085). 58 pp.

Currie, D.R., Dixon, C.D., Roberts, S.D., Hooper, G.E., Sorokin, S.J., Ward, T.M. (2009). Fishery-independent by-catch survey to inform risk assessment of the Spencer Gulf Prawn Trawl Fishery. Report to PIRSA Fisheries. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 121 pp.

Dixon, C.D., Svane, I., Ward, T.M. (2005). Monitoring and assessment of by-catch and by-product species of the Spencer Gulf Prawn Fishery. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. RD04/0249. SARDI Research Report Series No. 102. 62 pp.

Ferrell, D., Sumpton, W. (1998). Assessment of the Snapper fishery in Queensland and NSW. Final report to FRDC for Project 93/074.

Fowler, A.J., 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., McGlennon, D. (2011). Variation in productivity of a key snapper *Chrysophrys auratus*, fishery related to recruitment and fleet dynamics. Fisheries Management and Ecology 18(5): 411-423.

Fowler, A.J., McGarvey, R., Feenstra, J.E., Jackson, W.B., Jennings, P.R. (2005). Snapper (*Pagrus auratus*) Fishery. Fishery Assessment Report to PIRSA for the Marine Scalefish Fishery Management Committee. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, RD03/0068-2. 99 pp.

Fowler, A.J., McGarvey, R., Feenstra, J.E., Jackson, W.B. (2007). Snapper (*Pagrus auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-1. SARDI Research Report Series No. 224. 90 pp.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E., Jackson, W.B. (2010). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-2. SARDI Research Report Series No. 473. 109 pp.

Fowler, A.J., McGarvey. R., Carroll, J., Feenstra, J.E., Jackson, W.B., Lloyd, M.T. (2016). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-4. SARDI Research Report Series No. 930. 82pp.

Fowler, A.J., Hamer, P.A., Kemp, J. (2017). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely-dispersed, coastal fishery species. Fisheries Research 189: 77-94.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

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. (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.

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

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Hamer, P.A., Conron, S. (2016). Snapper stock assessment 2016, Fisheries Victoria Science Report Series 10, Fisheries Victoria, Queenscliff.

Holme, N.A., Mcintyre, A.D. (1971). Methods for the Study of Marine Benthos.' Blackwell Science: Oxford, UK.

McGlennon, D., Jones, G.K. (1997). Snapper (*Pagrus auratus*). South Australian Fisheries Assessment Series No. 97/07. 59 pp.

McGlennon, D., Jones, G.K., Baker, J., Jackson, W.B., 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: 669-677.

McGlennon, D. (2003). The fisheries biology and population dynamics of Snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. PhD Thesis, University of Adelaide, Adelaide, South Australia. 212pp.

Parsons, D.M., Sim-Smith, C.J., Cryer, M., Francis, M.P., Hartill, B., Jones, E.G., Le Port, A., Lowe, M., McKenzie, J., Morrison, M., Paul, L.J., Radford, C., Ross, P.M., Spong, K.T., Trnski, T., Usmar, N., Walsh, C., Zeldis, J. (2014). Snapper (*Chrysophrys auratus*): a review of life history and key vulnerabilities in New Zealand. New Zealand Journal of Marine and Freshwater Research 48: 256-283.

Rogers, T.A., Clarke, T., Drew, M.J., Bussell, J., Huveneers, C., Fowler, A.J. Comparison of methodologies to monitor the abundance of 0+ Snapper (*Chrysophrys auratus*: Sparidae).

Saunders, R.J. (2009). The reproductive biology and recruitment dynamics of Snapper, *Chrysophrys auratus*. PhD Thesis, University of Adelaide, Adelaide, South Australia, 154 pp.

Saunders, R.J., Fowler, A.J., Gillanders, B.M. (2012). The use of food resources by 0+ snapper, *Chrysophrys auratus*, from northern Spencer Gulf, South Australia. Marine and Freshwater Research. 63(8): 680-686.

Sim-Smith, C.J., Jeffs, A.G., Radford, C.A. (2012). Variation in the growth of larval and juvenile Snapper, *Chrysophrys auratus* (Sparidae). Marine and Freshwater Research 63: 1231-1243.

Sumpton, W., 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.

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., Schult, D., Hewitt, J.E., Talley, D. (2002). Habitat structure in soft-sediment environments and abundance of juvenile Snapper *Pagrus auratus*. Marine Ecology Progress Series 245: 273-280.

6.6 Appendices

6.6.1 Maps for juvenile Snapper surveys

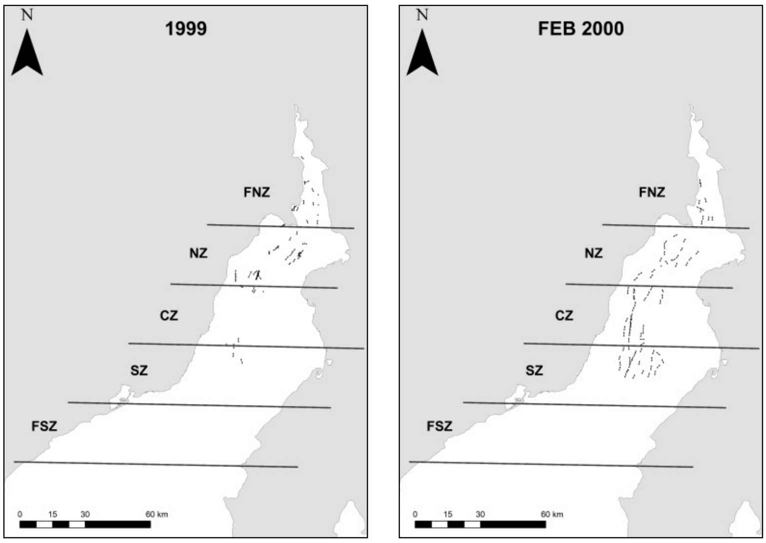


Fig. A6.1. Maps of Northern Spencer Gulf showing the transects that were sampled for juvenile Snapper in February 1999 and 2000. The lines on each map show the lengths and orientation of the transects sampled in each year. The division of the region into zones is also shown.

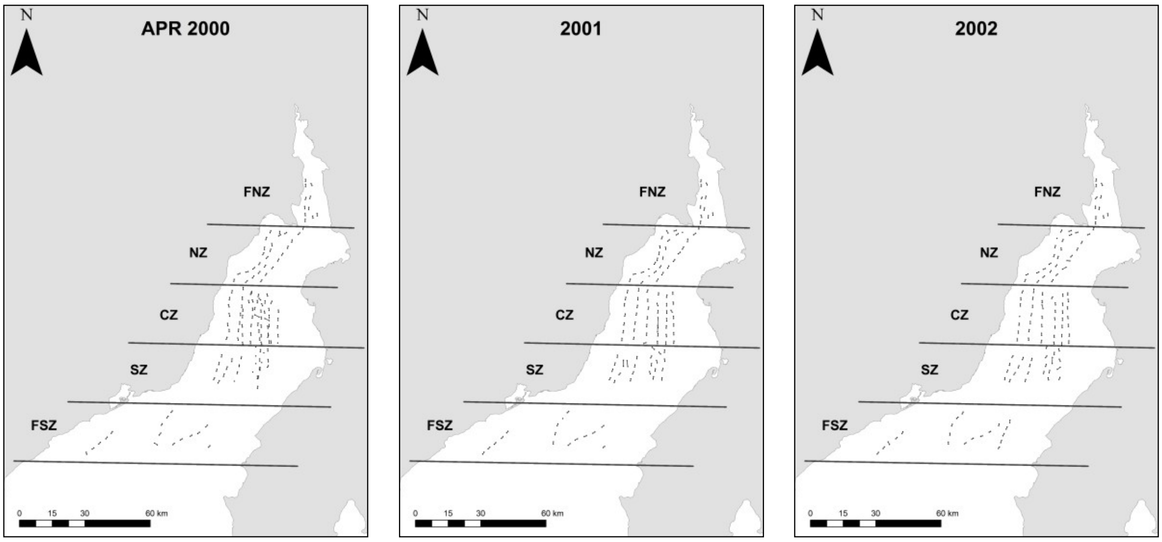


Fig. A6.2. Maps of Northern Spencer Gulf showing the transects that were sampled for juvenile Snapper in April of each year from 2000 to 2010. The lines on each map show the lengths and orientation of the transects sampled in that year. The division of the region into zones is also shown.

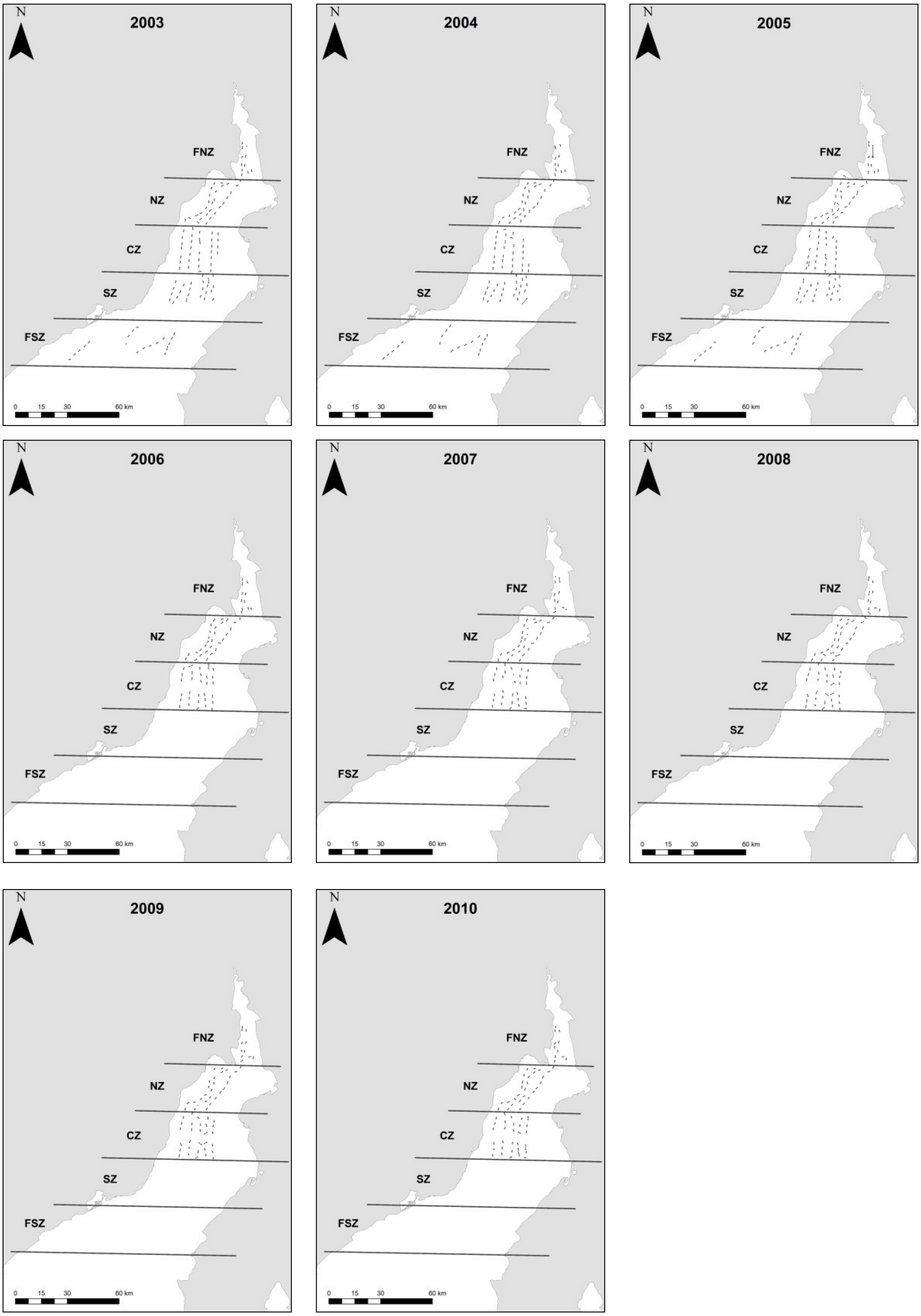


Fig. A6.2. continued.

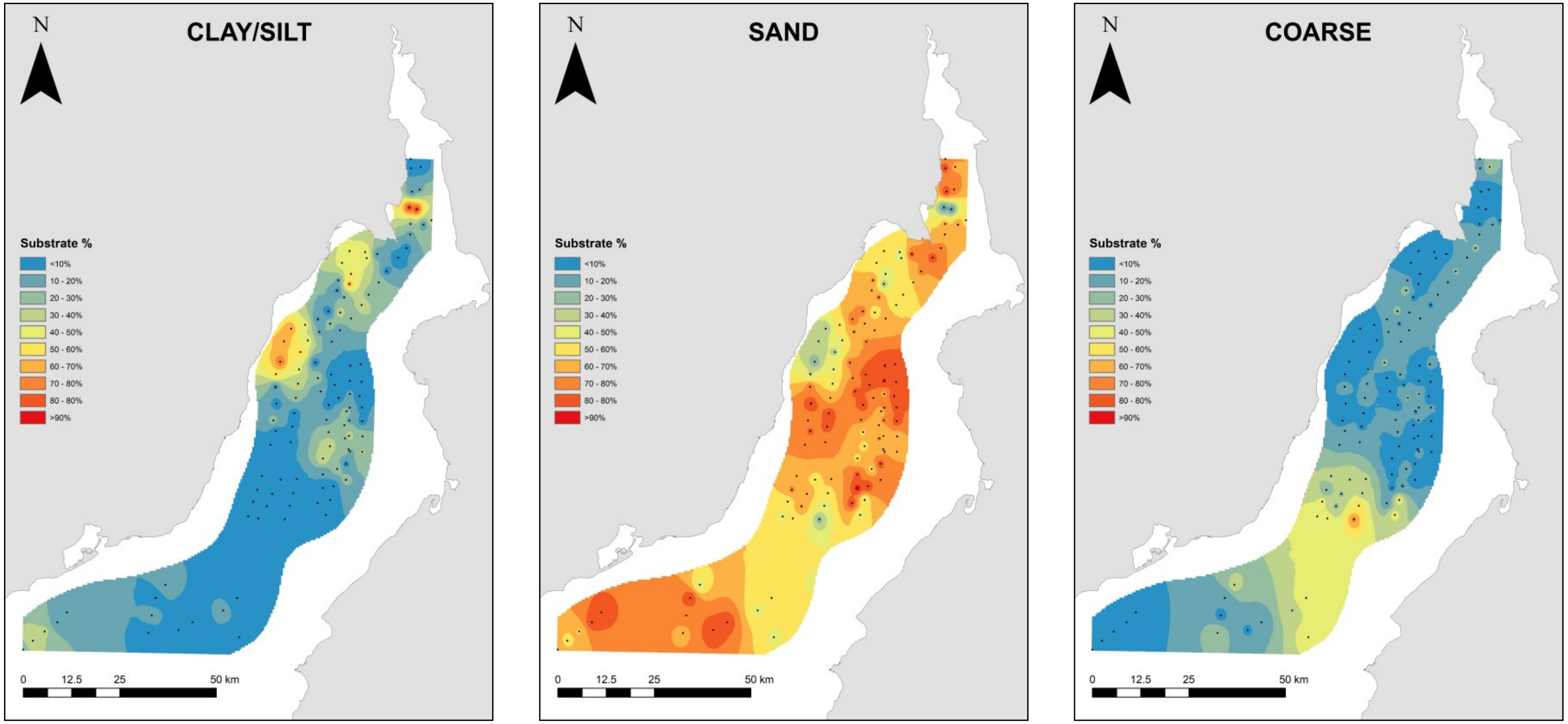


Fig. A6.3. Maps of Northern Spencer Gulf showing the results of the sediment analysis undertaken in 2000. The maps show the percentage contribution by weight of clay/silt, sand and coarse sediment throughout the region.

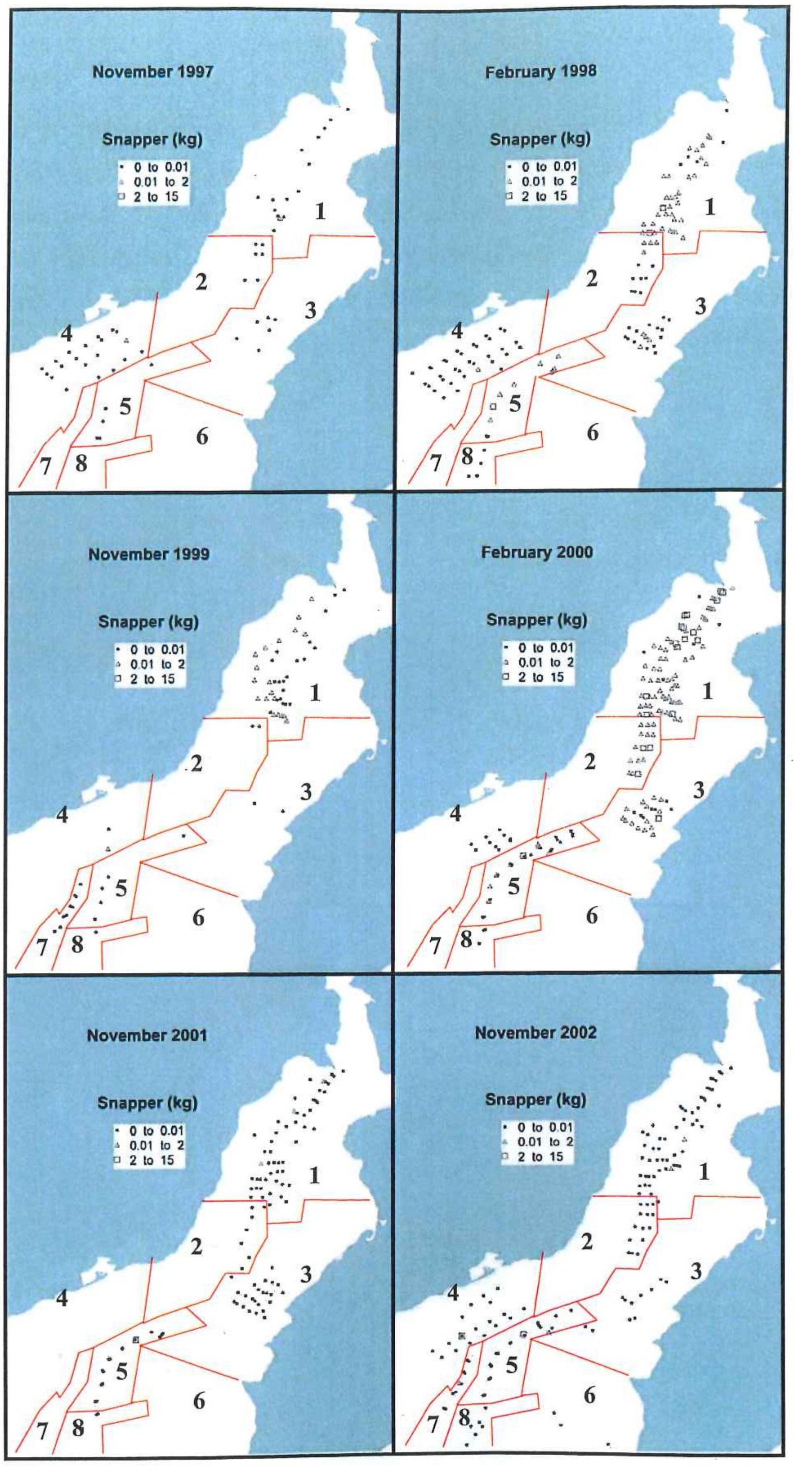


Fig. A6.4. Maps of Spencer Gulf showing the location of by-catch survey shots and the biomass of Snapper captured during six different surveys (from Dixon et al. 2005).

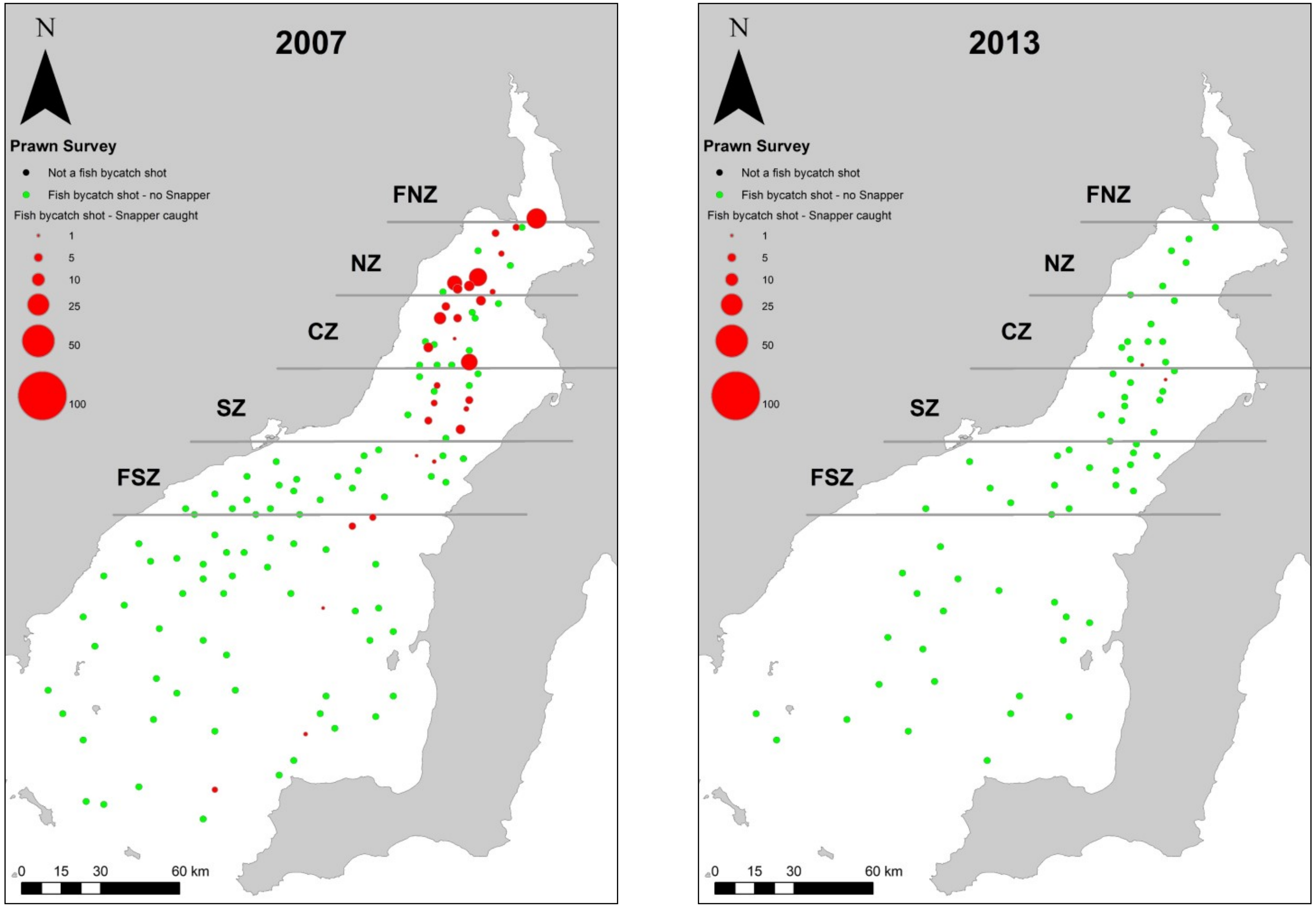


Fig. A6.5. Maps of Spencer Gulf showing the locations of by-catch survey shots and the numbers of 1+ Snapper captured during surveys in February 2007 and 2013. The zones considered in the otter trawl surveys for 0+ Snapper are indicated.

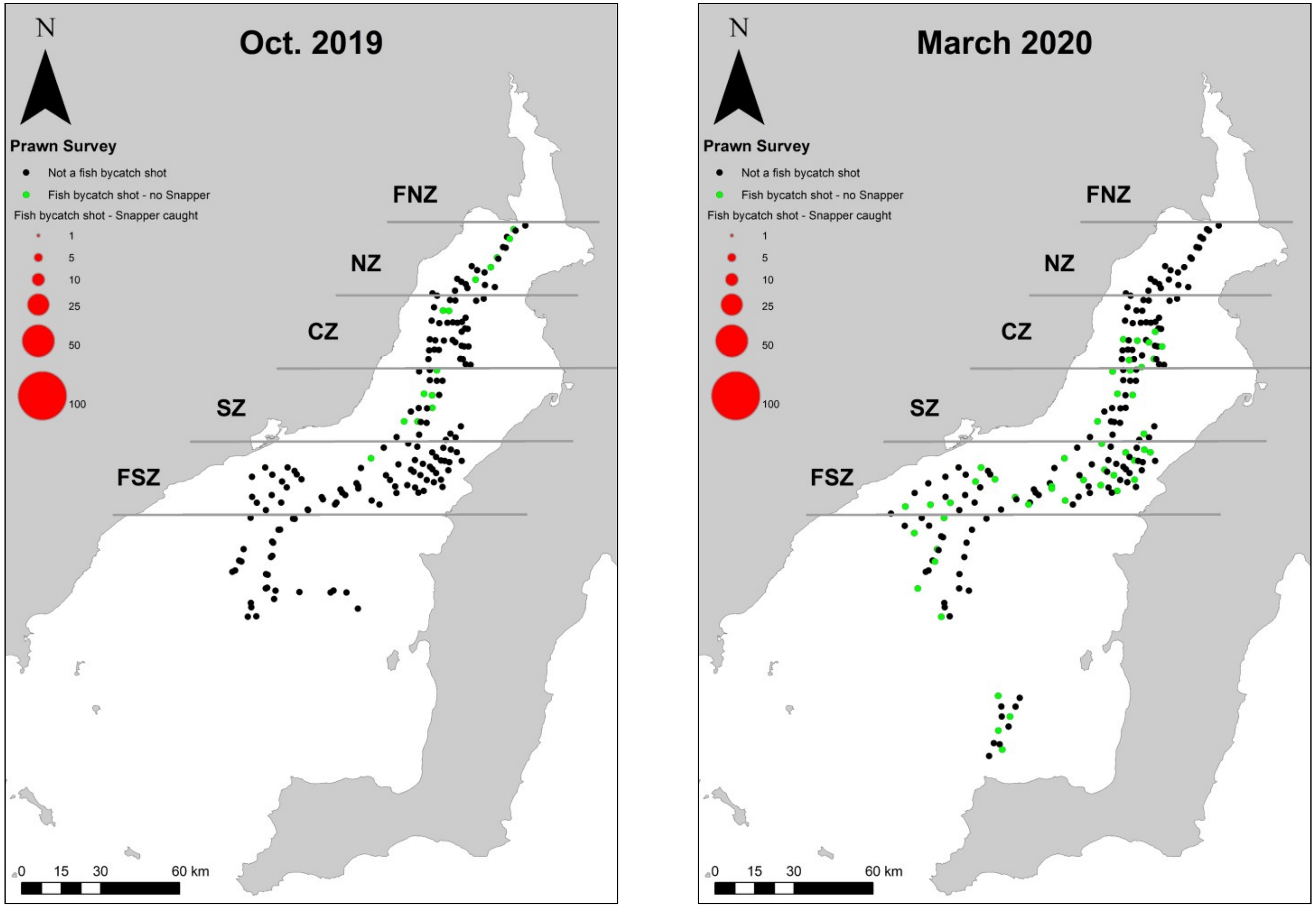


Fig. A6.6. Maps of Spencer Gulf showing the location of stock assessment survey shots for prawns, those for which the finfish by-catch was considered, and the number of juvenile Snapper captured in October 2019 and March 2020. The zones considered in the otter trawl surveys for 0+ Snapper are indicated.

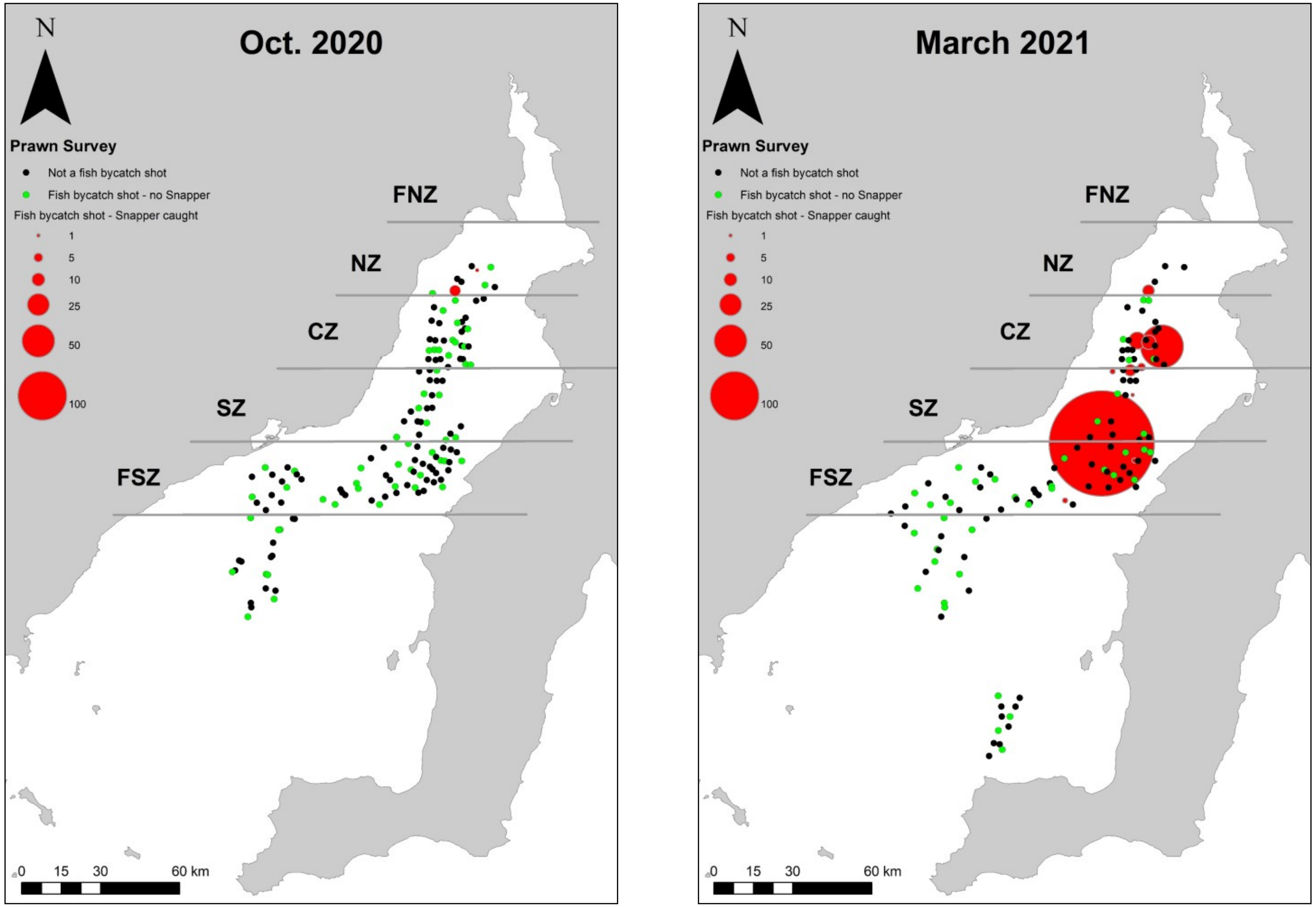


Fig. A6.7. Maps of Spencer Gulf showing the location of stock assessment survey shots for prawns, those for which the finfish by-catch was considered, and the number of juvenile Snapper captured in October 2020 and March 2021. The zones considered in the otter trawl surveys for 0+ Snapper are indicated.

7. RECRUITMENT VARIATION - ENVIRONMENTAL INFLUENCES

Anthony Fowler

7.1 Introduction

A long-recognised characteristic of marine fish populations is that recruitment of juvenile fish can display significant inter-annual variation (Hjort 1914, Cushing 1988, Cushing 1990). In many cases this is likely to relate to the reproductive/recruitment processes, whereby immense numbers of eggs are spawned and broadcast into the water column, whose probability of survival through the embryonic and larval development phases is minute. Nevertheless, relatively minor variation in their rates of survival between years can culminate in differences, in orders of magnitude, in the numbers of 0+ fish that recruit to the populations (Cushing 1988, Doherty and Fowler 1994a,b). Such variable recruitment can dominate the demographic processes that drive the population dynamics and fishery productivity and account for the variation over time in sizes and ages of the fish in the populations (Doherty and Fowler 1994a).

It is evident from trawl surveys that have been done throughout Australasia, including the south-east region of Australia, that Snapper, *Chrysophrys auratus*, experiences significant inter-annual variation in recruitment (Chapter 6, Francis 1993, 1995, Fowler and Jennings 2003, Hamer and Jenkins 2004, Sumpton and Jackson 2005, Bessell-Brown et al. 2020). The on-going consequence of such variability is that Snapper populations involve strong and weak year classes, which drive population dynamics and variable fishery productivity (Fowler and McGlennon 2011, Fowler et al. 2013). It would be invaluable to develop some understanding of the relationship between recruitment and environmental influences as a means of predicting fishery productivity (Francis 1993, 1995, Fowler and Jennings 2003, Hamer and Jenkins 2004, Murphy et al. 2012, 2013, Sim-Smith et al. 2012). The issue of environmental influences on Snapper recruitment was addressed in this chapter for the Snapper fisheries of Spencer Gulf/West Coast Stock (SG/WCS) and the Gulf St. Vincent Stock (GSVS). This was done by addressing the specific objectives: of generating a time-series of annual recruitment rates for each of the SG/WCS and the GSVS; developing time series of estimates of environmental variables for appropriate time periods and spatial scales relevant to the recruitment data sets for the two stocks; and assessing whether there were any relationships between the recruitment time series and the environmental variables for both stocks.

7.2 Materials and methods

7.2.1 Recruitment time series

The quantitative estimates of time series of recruitment that were considered in this study were generated by the SnapEst fishery assessment model during the stock assessment that was undertaken in 2020 (Fowler et al. 2020). SnapEst is a dynamic, spatial, age- and length-structured model that integrates data from several sources that include: commercial, recreational and charter fishery statistics; population size and age structures; and most recently, estimates of spawning biomass determined using the daily egg production method (McGarvey and Feenstra 2004). For the assessment undertaken in 2020, SnapEst was modified to operate at the spatial scale of stock, i.e., for the SG/WCS, GSVS, and for the population of the southeast region of the State (SE Region) (Fowler et al. 2020). The model integrated the input data streams to produce maximum likelihood estimates of the four fishery performance indicators: fishable biomass; numbers of recruits; harvest fraction; and egg production. Of these, here the time series for the annual estimates of recruitment generated by the SnapEst model were of primary interest. They were calculated largely based on annual age structures that had been generated at the regional scale (Chapter 9) and covered the time-period of 1983 to 2017. For the SG/WCS, the regional age structures for Northern Spencer Gulf (NSG) and Southern Spencer Gulf (SSG) were considered in the model, whilst for the GSVS, the age structures from both Northern Gulf St. Vincent (NGSV) and Southern Gulf St. Vincent (SGSV) were integrated into the model. The annual age structures for Snapper populations in each region had been generated for numerous years between 2000 and 2020, based on estimates of size and age for fish accessed through SARDI's commercial market sampling program (Chapter 9, Fowler et al. 2016). These fish had primarily been captured by the commercial sector of South Australia's Marine Scalefish Fishery and were mainly accessed at the SAFCOL wholesale fish market in Adelaide (Chapter 9).

7.2.2 Physical environmental time series

Time series of physical environmental data, i.e., sea surface temperature (SST), wind and rainfall were accessed from several different sources. SST data were accessed at two spatial and temporal scales. First, to assess whether the physical marine environment of the gulf region of South Australia had changed through the 20th and 21st Centuries, model-reconstructed monthly estimates of SST were accessed for the period of 1900 to 2021 (Huang et al. 2017) and used to calculate a time series of average annual estimates of SST. Also, SST data were considered at a smaller spatial scale, a finer temporal resolution and for a shorter period. For each of five regions, two located in each of Spencer Gulf and Gulf St. Vincent and the fifth located in the SE Region (Fig. 7.1), SST data were accessed for the period from 1981 to 2021. Daily night-time mean estimates of SST were derived from a multi-satellite SST product based on observations from AVHRR instruments on all available NOAA polar-orbiting satellites (Saha et al. 2018). Data from 1981 to 1993 were obtained at the 4 km resolution, whilst those from 1993 onwards were obtained at 0.02° resolution (i.e., approximately 37 m). Only high-quality SST data were used, to avoid the influence of cloud contamination.

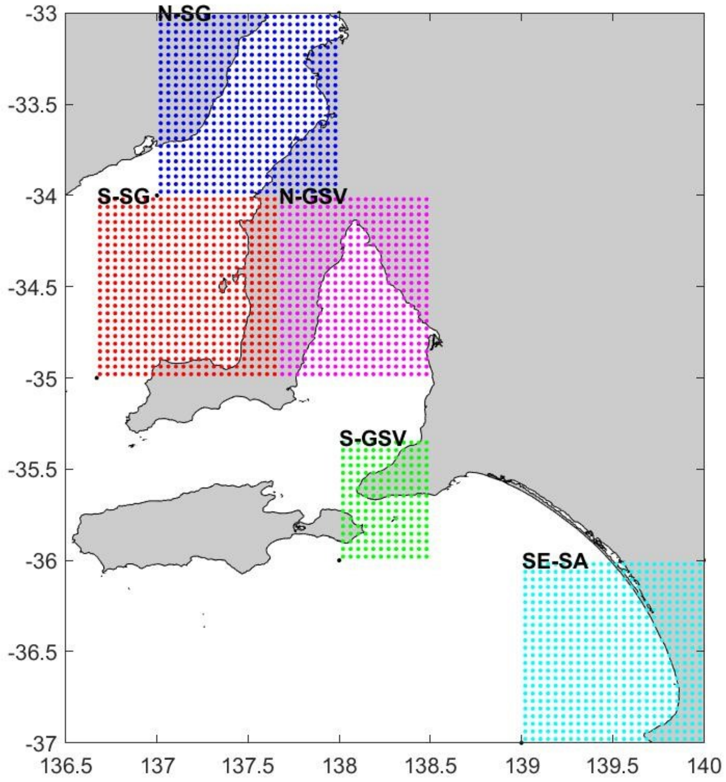


Fig. 7.1. Map of the gulf region and SE Region of the South Australian coastline showing the five regions for which SST data were accessed from satellite imagery from 1981 to 2021.

For NSG and NGSV, relationships between SST and recruitment were assessed using the finer-scale SST data. The former region supports the nursery areas for the SG/WCS as well as the places where reproduction and early life history processes are assumed to occur (Chapter 6). For the GSVS, there is less known about the spatial aspects of reproduction and recruitment, so here it was assumed that these processes occurred in NGSV, based on the understanding for Spencer Gulf. For both regions, the daily estimates of SST from satellite imagery were used to calculate the average temperatures from all days in December, January and February in each summer. These months incorporate the main period for reproduction, early life history processes and settlement for Snapper in South Australia, as determined from the microstructure of otoliths of 0+ fish collected in NSG (Chapter 8, Fowler and Jennings 2003, Saunders 2009, Fowler et al. 2010, Saunders et al. 2012). Most of the captured 0+ recruits were spawned in December and January, whilst the timing of settlement extended into February (Chapter 8, Fowler and Jennings 2003, Saunders 2009). For each of NSG and NGSV, the time series for recruitment were compared with the annual estimates of summer SST using correlation analyses.

For NSG, the average monthly wind data were accessed from the Bureau of Meteorology for weather station number 18120 (located at Whyalla adjacent to NSG), for the years of January 1984 to December 2012. The data included the average monthly wind speed (V) and direction (ϕ). These wind data were divided into the V-wind or meridional (north-south) component and the U-wind or zonal (east-west) component as; V-wind = V*(cos ϕ), and U-wind = V*(sin ϕ), respectively. The annual summer averages (across December, January, and February) for both the V-wind and U-wind components were calculated. These data were then compared with the recruitment history time series using correlation analyses. Furthermore, the annual time series of V-wind and U-wind components for each of December and January in every year were compared with the recruitment time series. For NGSV, wind data from Adelaide airport (weather station 23034) were accessed for the period of January 1986 to July 2013. These data were provided at a three-hour period. They were summarised and analysed as for the wind data for NSG.

Data on rainfall, as measured at Whyalla and at Adelaide airport were also accessed from the Bureau of Meteorology. For NSG, the time series considered was for the years of 1984 to 2012, whilst for NGSV the years were 1987 to 2013. For each region, the time series of average rainfall across the three months of December, January and February was compared with the recruitment history using correlation analysis.

7.3 Results

7.3.1 Recruitment time series

Spencer Gulf/West Coast Stock

The age structures for Snapper in South Australia retain useful information about historic recruitment rates. The populations consisted of multiple age classes with fish from three to >30 years of age (Chapter 9). The age structures reflected that the contributions of different age classes to the population were highly variable. Such variation in age class strength ultimately related to strong and weak recruitment year classes that persisted in the populations for years and even decades. Historic age structures for NSG that were developed in 1991 and 1994 had suggested that the 1979-year class was particularly strong, whose influence persisted in fishery catches until 2002 (McGlennon and Jones 1997, McGlennon et al. 2000). There was also an indication that the 1973-year class was relatively strong. Then, the age structures from 2000 up to 2015, indicated that the 1991, 1997 and 1999-year classes each made considerable contributions to fishery catches over numerous years (Chapter 9, Fowler 2000, 2002, Fowler et al. 2003, 2007, 2010, 2013, 2016). Similarly, for SSG the age structures from 2000 to 2014 were also dominated by the 1991, 1997 and 1999-year classes.

The numerous age structures that were developed throughout the 2000s for NSG and SSG (Chapter 9) were integrated by the SnapEst model to contribute to generating recruitment time series for the whole SG/WCS for the 35-year period from 1983 to 2017 (Fig. 7.2a). This time series indicates that generally the numbers of new recruits to the stock were low, i.e. <325,000 recruits.year^{-1}, with more than half the years receiving <100,000 recruits.year^{-1}. Even though such low recruitment occurred throughout the 1980s, the rates through this period were marginally higher than the very low estimates for the years from 1992 to 1996. Low recruitment rates were also estimated for all years throughout the 2000s, particularly from 2008 to 2013 for which the average rate was exceptionally low at 44,743 recruits.year^{-1}. In contrast, there were three exceptional year classes for which estimated numbers of recruits were many times, if not several orders of magnitude, higher than for the other years. These super year classes recruited in 1991, 1997 and 1999 (Fig. 7.2a). For these three years, the model-estimated numbers of recruits.year^{-1} were 2,005,890, 1,111,860 and 840,519, respectively. No such super year class has recruited to the SG/WCS since 1999, which made the 2000s the longest period without one.

For the SG/WCS, by considering the quantitative estimates of recruitment from SnapEst along with the qualitative indications of year class strength from the age structures for prior to 1983, it is apparent that throughout the 47-year period from 1970 to 2017, there were at best five and possibly only four super year classes. The certain ones recruited in 1979, 1991, 1997 and 1999, whilst the ambiguous one was for 1973.

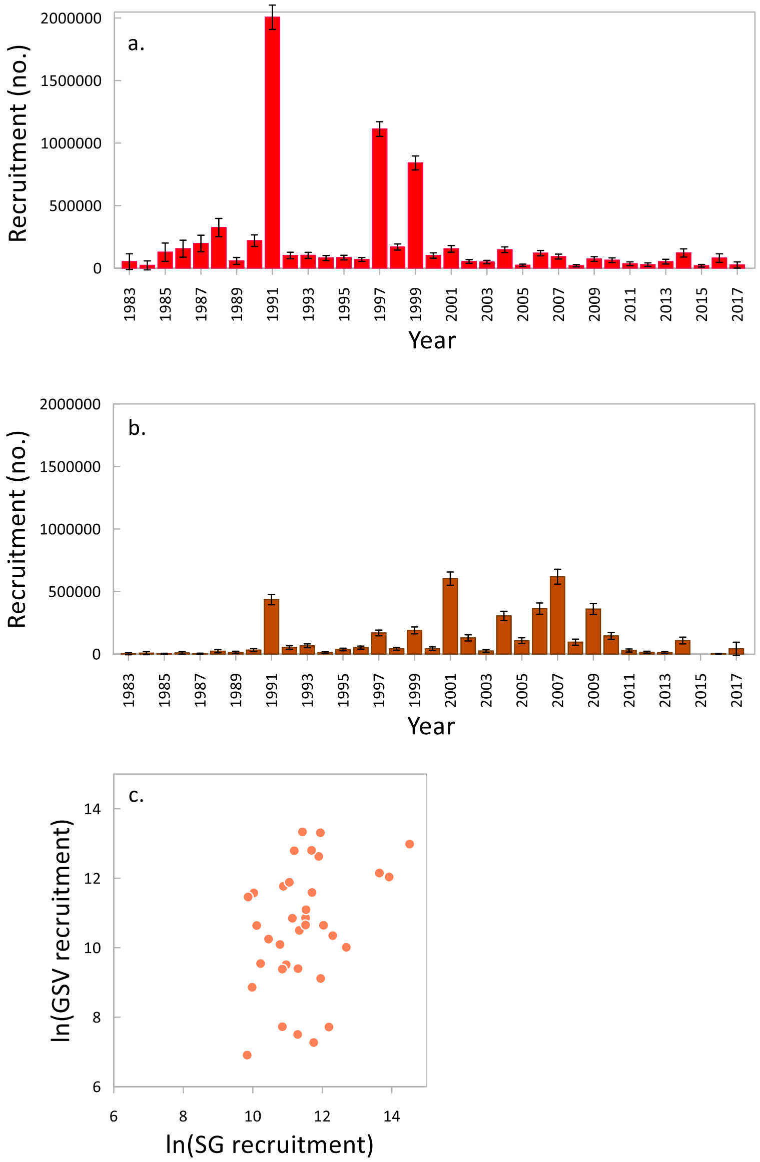


Fig. 7.2. Estimates of annual recruitment rates (+CL) from the SnapEst model in 2020 (Fowler et al. 2020). a. for the SG/WCS. b. for the GSVS. c. scatterplot of the ln transformed recruitment rates for the GSVS against those for the SG/WCS.

Gulf St. Vincent Stock

The age structures for the regional populations of NGSV and SGSV indicate that during the 1990s, the populations were dominated by the 1991, 1997 and 1999-year classes, as was the case for Spencer Gulf (Chapter 9). However, there were several differences between the age structures from the two gulfs. First, the age structures for the regional populations of Gulf St. Vincent showed no compelling evidence that the 1979-year class had been an exceptional year class (Fowler 2000, 2002, Fowler et al. 2003). Secondly, for the year classes from 2000 onwards, there were numerous strong year classes evident in the age structures for both NGSV and SGSV.

Throughout the 1980s for the GSVS, estimates of recruitment from the SnapEst model were exceptionally low, i.e. generally <20,000 recruits.year^{-1} (Fig. 7.2b). For the 1990s, there were several strong year classes, i.e. in 1991, 1997 and 1999, for which the rates were 434,986, 168,567 and 189,018 recruits.year^{-1}, respectively. For the 2000s, however, the situation was very different, as the recruitment time series was essentially divisible into two periods. Up to 2009 there were five strong year classes, i.e. in 2001, 2004, 2006, 2007 and 2009, for which the rates ranged from 304,897 to 618,628 recruits.year^{-1}. In comparison, from 2011 to 2017, the recruitment rates were much lower, with the average rate across these six years of 29,503 recruits.year^{-1}, which was the longest period of low recruitment for the GSVS since the 1980s.

Comparison between stocks

From comparison of recruitment time series between stocks there are a number of similarities and some differences (Fig. 7.2a,b). Overall, recruitment to the SG/WCS was higher, receiving 41% more recruits than did the GSVS. For the former stock, recruitment was heavily concentrated in the three years of 1991, 1997 and 1999, which accounted for 57% of recruits to this stock across the 35 years. For the GSVS, recruitment rates were generally lower. The highest number in any year was 618,628, which was only 30% of the highest for the SG/WCS. Alternatively, for the GSVS there were more years for which recruitment was relatively high. Despite these differences, there was a marginally significant positive correlation between the time series ($r = 0.3362$, $df = 33$, $p = 0.0483^*$) (Fig. 7.2c), which indicated some consistency in the timing of recruitment between stocks. Whilst both stocks shared the same strong year classes, there was a change that occurred in the scale of the sizes of the strong year classes. During the 1990s, the strong year classes of 1991, 1997 and 1999 were larger for the SG/WCS than for the GSVS. Alternatively, throughout the 2000s, both stocks shared the same strong year classes in 2001, 2004, 2006, 2007 and 2009, but the numbers were considerably higher for the GSVS. This synchrony in recruitment rates across years suggests that the factors that determined year class strength operated at a broad geographic scale. Nevertheless, the change in scale that occurred between stocks around 2000 suggests the influence of a major demographic process that simultaneously affected both stocks.

7.3.2 Physical Environmental Data

From model-reconstructed estimates of SSTs for the years of 1900 to 2020 for South Australia's gulf region, annual averages were calculated for calendar years. Until the early 1950's, the estimates were variable but nevertheless showed no long-term change (Fig. 7.3). However, for the 70 years from then until 2020 there has been a gradual increase over time. The significant linear relationship of: [SST = (0.015Year) – 13.1054] ($r^2 = 0.6637$, df = 68, p<0.001) indicates an average increase of 0.015°C per year. For the broad gulf region of South Australia, equating to an increase of approximately 1°C in SST since the early 1950s.

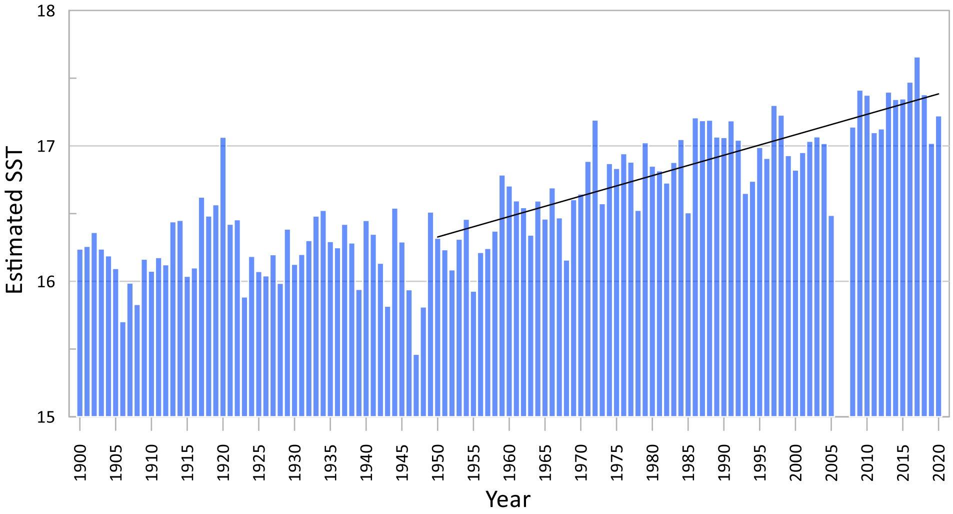


Fig. 7.3. Estimates of model-reconstructed estimates of SST for South Australia's gulf region for the period of 1900 to 2020. The linear line-of-best-fit from regression analysis for the years of 1950 to 2020 is indicated.

Empirical data for daily night-time estimates of SST from satellite imagery were accessed for five South Australian coastal regions for the calendar years of 1982 to 2020 (Fig. 7.4). The average summer SSTs were calculated across the months of December, January and February in each summer. There were clear differences amongst regions in the time series. The summer night-time SSTs in NSG (range amongst years 20.0 – 23.7°C) were clearly higher than those for SSG (18.6 – 21.6°C) (Fig. 7.4a). Furthermore, the summer SSTs were always warmer for NGSV (19.0 – 22.4°C) than for SGSV (17.3 – 20.2°C) (Fig. 7.4b). The estimates for the SE Region were the lowest (15.5 – 18.4°C). The temporal patterns of variation were similar amongst regions, particularly for the four gulf regions, which were highly correlated, with the strength of the correlations lowest between the gulf regions and the SE Region (Table 7.1).

For each region there was an increase in estimates of summer SSTs over time, which was most evident during the early 1990s. Throughout the 2000s, the trends were relatively flat. The apparent increase here may relate to the change in methodology that occurred around this time. As such, there is some uncertainty surrounding the apparent increases in the temporal trends for SST for the different regions. Nevertheless, it is likely that the inter-annual variability evident in each regional time series generally reflects real differences that occurred between years.

The time series of estimated recruitment for the SG/WCS was compared with the regional estimates of SST from satellite imagery for NSG using correlation analysis (Fig. 7.5a). The datasets were not significantly correlated (r = -0.0654, n = 35, df = 33, p = 0.7107^{ns}). The time series for SSTs demonstrate considerable inter-annual variation, nevertheless, the three strong recruitment year classes are not associated with estimates of SST that were particularly different from those for other years (Fig. 7.5a). In comparison, for the GSVS, there was a significant positive correlation between the ln transformed recruitment data and the estimates of SST for NGSV (r = 0.407, n = 35, df = 33, p = 0.0152*) (Fig. 7.5b).

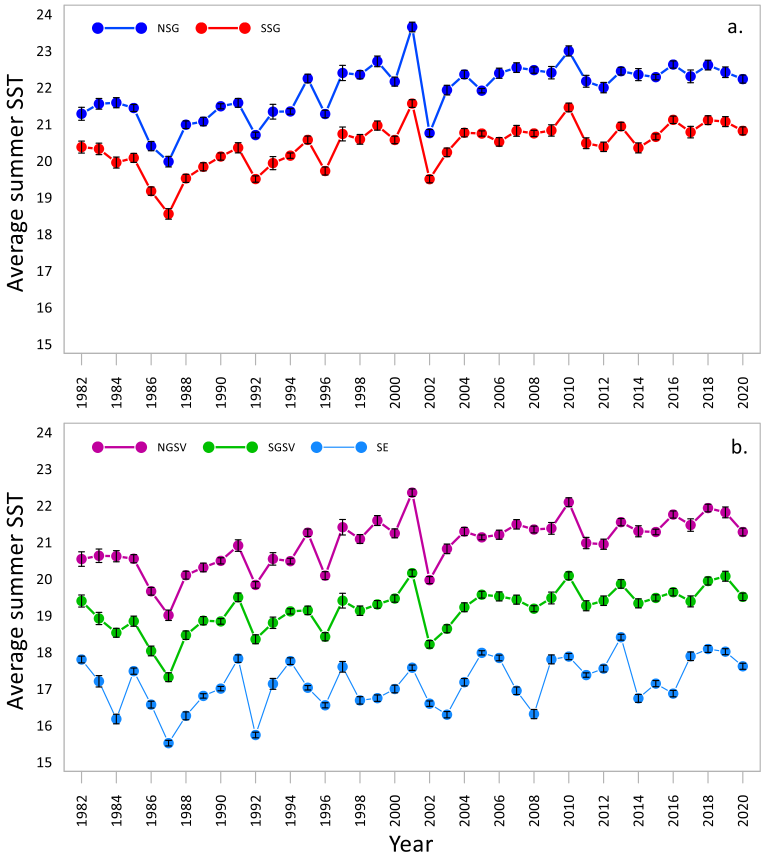


Fig. 7.4. Time series of average (±SE) summer night-time SSTs from satellite imagery for South Australian regions. a. NSG and SSG. b. NGSV, SGSV and SE.

Table 7.1. Summary of correlation coefficients calculated for comparisons amongst the five time-series of regional summer SSTs from satellite imagery (significance level at p = 0.05 is 0.3345).

	NSG	SSG	NGSV	SGSV	SE
NSG	1				
SSG	0.96	1			
NGSV	0.98	0.98	1		
SGSV	0.87	0.95	0.93	1	
SE	0.52	0.67	0.62	0.79	1

For the SG/WCS there were no significant correlations between the recruitment history and the average wind data in each of December, January and February, as well as for the whole summer averaged across the three months (Table 7.2). This was the case for both the V-wind (north-south) and the U-wind components (east-west). There was also no correlation between the recruitment data and the estimates of average summer monthly rainfall across the months of December, January and February (Table 7.2).

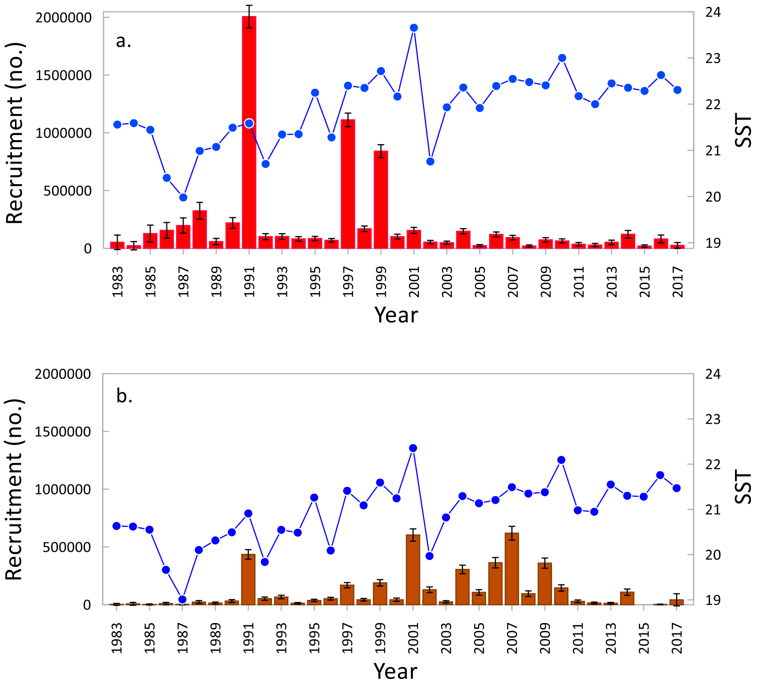


Fig. 7.5. Comparison between recruitment time-series and the summer SSTs. a. recruitment time series for the SG/WCS from the SnapEst model and summer SSTs for NSG. b. recruitment time series for the GSVS and SSTs for NGSV.

For the GSVS, the results with respect to lack of significant correlations between recruitment and physical environmental data were similar to those for the SG/WCS except that there was a significant positive correlation between the U-wind component in February and the recruitment time series (Table 7.2). This positive relationship suggests that, on average, stronger westerly winds during February resulted in higher year class strength for that summer ($p = 0.0118$). Furthermore, for GSVS, although the correlation coefficient between recruitment and average summer monthly rainfall was not significant, the coefficient was relatively high and was associated with a low probability ($p = 0.0635$) (Table 7.2), suggesting a possible weak relationship.

Table 7.2. Summary of results from correlation analyses between recruitment histories for the two stocks and physical environmental variables for Northern Spencer Gulf and Northern Gulf St. Vincent.

Stock	Years		df	V-wind	U-wind	rainfall
SG/WCS	1984-2012	Dec	25	-0.1371^{ns}	0.2714^{ns}	-
		Jan	26	-0.0457^{ns}	-0.2463^{ns}	-
		Feb	25	0.2686^{ns}	-0.158^{ns}	-
		Summer	26	-0.1397^{ns}	-0.0682^{ns}	-0.0543^{ns}
GSVS	1986-2013	Dec	26	-0.0807^{ns}	-0.0074^{ns}	-
		Jan	26	-0.0066^{ns}	0.1661^{ns}	-
		Feb	26	0.2690^{ns}	0.4211*	-
		Summer	26	0.0570^{ns}	0.3135^{ns}	-0.3617^{ns}

7.4 Discussion

7.4.1 Recruitment time series

In the stock assessment undertaken in 2020, the recruitment time series were generated by the SnapEst model for each of the SG/WCS and the GSVS (Fowler et al. 2020). These were based largely on regional, annual population age structures developed between 2000 and 2019 (Chapter 9). The recruitment time series for the two stocks demonstrated considerable variation in year class strength, between which there was some synchrony.

Variable age class strength in age structures is a characteristic of some Snapper populations (Fowler and McGlennon 2011, Hamer and Conron 2016). It is a manifestation of inter-annual variation in recruitment of the 0+ juveniles to the benthic populations (Fowler and Jennings 2003, Hamer and Jenkins 2004, Fowler and McGlennon 2011). Over numerous years there has been a considerable focus on understanding the nature of this variability (Francis 1993, Fowler and Jennings 2003, Hamer and Jenkins 2004). Studies in Victoria and New Zealand have indicated that year class strength is established during the larval phase of the life history (Zeldis et al. 2005, Hamer et al. 2010, Murphy et al. 2012, 2013). This chapter focussed on the two main South Australian stocks, particularly the northern regional population of each stock. For the SG/WCS, the northern region of Spencer Gulf is where reproduction, early life history processes and recruitment to nursery areas occur (Chapters 2, 3, 6). Throughout the 47-year period from 1970 to 2017, the recruitment rates for this stock were generally low. There were four definite strong year classes and possibly a fifth. For the period of 1983 to 2017, several physical environmental datasets were compared with the recruitment time series, but there were no significant correlations. There were no obvious environmental perturbations that occurred in 1991, 1997 and 1999 that could account for the super year classes in those years. For the GSVS, there were more strong year classes in the recruitment time series. There were also several correlations with physical environmental data, i.e., with SST, with the wind data during February, and a possible weak relationship with rainfall.

These results for NSG and NGSV are somewhat contradictory. They indicate that the environmental influence on recruitment is not a simple response to a single physical environmental variable such as SST, as considered by previous studies (Francis 1993, Fowler and Jennings 2003). Rather, the lack of relationships for the SG/WCS and weak ones for GSVS suggest that the environmental drivers for variable recruitment of Snapper are likely to be complex and involve a combination of factors. Here it is worth considering how environmental factors could influence larval survivorship; and evidence of earlier studies of such environmental influences.

7.4.2 Possible influences on larval survivorship

Larval culture experiments have empirically assessed the influence of water temperature on the development of Snapper larvae (Fielder et al. 2005). The survivorship and growth of larvae that were reared at 15, 18, 21, 24, 27, 30 and 33°C were compared and physiological tolerance limits identified (Fielder et al. 2005). All larvae died that were reared at 27, 30 and 33°C. Furthermore, for those reared at 15°C, the rate of swim bladder inflation was low, indicating that development was impaired. Water temperatures in the range of 18-24°C resulted in the highest rates of production of viable larvae. As growth rates were strongly influenced by water temperature, Fielder et al. (2005) concluded that of the preferred range of 18-24°C for larval development, the warmer temperature was optimal for growth and survival. If considered in the context of the natural environment, these results suggest that Snapper larvae reared in higher temperatures would have faster growth and shorter pre-settlement duration. This could lead to higher survivorship because of the shorter period of vulnerability to planktonic predation (Houde 1987, 1989, Sogard 1997). Empirical evidence in support of this is that abundances of larval Snapper have been related to growth rates, i.e., the years of fastest larval growth also had higher survivorship (Sim-Smith et al. 2012, Murphy et al. 2013).

The text above identifies how physiological development of Snapper larvae is directly influenced by water temperature which could influence survivorship in natural planktonic communities. However, such a result has not been demonstrated empirically. For the SG/WCS, there was no relationship between recruitment and SST. Other field studies have also demonstrated either no influence or only a minor effect of water temperature on larval survival and recruitment for Snapper (Zeldis et al. 2005, Murphy et al. 2012, 2013). The latter were studies on lower trophic systems and plankton dynamics done in Port Phillip Bay (Murphy et al. 2012, 2013) and the Hauraki Gulf, New Zealand (Zeldis et al. 2005). In both marine ecosystems, there was considerable variation amongst years in the plankton dynamics, in terms of zooplankton assemblage composition and biomass levels. This inter-annual variation also related to the numbers of the post-yolk sac Snapper larvae. The latter were most abundant in those years when secondary production resulted in higher abundances of their preferred prey-at-first-feeding such as copepod nauplii and copepodites. For the Hauraki Gulf, the higher primary and secondary production of the planktonic community in one year out of three was driven by stronger winds that caused greater vertical mixing through the water column, culminating in greater upper water productivity (Zeldis et al. 2005). This resulted in higher production of invertebrate and vertebrate zooplankton including Snapper larvae and their prey, despite that the three years had similar water temperature regimes. In Port Phillip Bay, inter-annual variation in survival of Snapper larvae and strength of 0+ recruitment was linked to diet relating to prey abundance and composition (Murphy et al. 2012). In the latter case, there was only a minor influence of water temperature on larval growth rates that were food-related (Murphy et al. 2013).

For teleost fish species, the susceptibility of first-feeding larvae to starvation is highly size-dependent. From consideration of 72 species of marine and freshwater teleosts, Miller et al. (1988) established that a 1 mm increase in size-at-hatch results in a two-day extension in the time that larvae have to find food before they reach a point of irreversible starvation. Since Snapper larvae hatch at approximately 2 – 3 mm TL (Pankhurst et al. 1991), they fall into the lower end in the range of size-at-hatching. This means they have minimal time to switch from endogenous to exogenous feeding. In culture, Snapper larvae that were starved from first-feeding, stopped swimming, lost condition very rapidly and starved to death in 3 – 4 days (Pankhurst et al. 1991). It is expected that under field conditions, in the presence of abundant ichthyo-planktivores, starving larvae would survive for considerably shorter times. Snapper larvae find their prey visually but have poor optical acuity and a short reactive distance. As such, for them to successfully capture sufficient prey, the latter would need to be relatively abundant and to be encountered frequently (Zeldis et al. 2005). This means that the environmental circumstances that would most likely produce the highest rates of survival of Snapper larvae would be those that produced high abundances of their prey.

There are numerous ways by which plankton dynamics, including the survival of Snapper larvae, could be influenced by water temperature. Clearly, water temperature influences the rate of physiological development of the larvae (Fielder et al. 2005), which affects their growth rates and pre-settlement duration (Sim-Smith et al. 2012). Pre-settlement duration determines the period of vulnerability to high predation rates in the plankton (Houde 1987, 1989, Sogard 1997). Water temperature must also influence primary and secondary production rates in the planktonic environment, thereby determining the availability of preferred prey for the developing Snapper larvae. Nevertheless, as demonstrated by the example for the Hauraki Gulf (Zeldis et al. 2005), there are also other physical environmental factors that influence planktonic productivity. Under such circumstances the influence of water temperature would likely be masked by a stronger physical influence. This suggests a complex, multi-factorial, inter-related physical and biological system that ultimately drives the variation amongst years in recruitment rates of Snapper and accounts for how relationships between recruitment of Snapper and water temperature have eventually broken down over time (Francis et al. 1997).

7.4.3 Lower trophic ecosystem function of Spencer Gulf

To date there has been only a single study on the lower trophic ecosystem functionality of Spencer Gulf (Middleton et al. 2013). That study demonstrated that seasonal variation in weather and oceanographic conditions strongly influences the chemistry of the waters of Spencer Gulf, driving the functionality of the lower trophic ecosystem. In summer, a strong thermo-haline front forms at the entrance to Spencer Gulf, which significantly reduces exchange with the waters of the continental shelf. At this time, residual currents are low. Furthermore, due to high rates of evaporation, the gulf waters increase in density. In autumn, the thermo-haline front breaks down causing the dense, highly saline water to pour out from the gulf. Also, there is an inflow of continental shelf water to the gulf and its northward movement along the western gulf coastline, and eastward into the southern region of the gulf. In response, phytoplankton concentrations begin to increase in the south-western part of the gulf. By late autumn, nutrient concentrations increase due to the import of nitrates from the shelf, which increases phytoplankton abundance. The winter circulation pattern continues the movement of waters with elevated concentrations of nutrients into the gulf resulting in higher levels of biomass of phytoplankton along the western coastline and eastwards across the gulf. This input of nutrients from continental shelf waters through autumn, winter and spring represents the primary source of nutrients to Spencer Gulf, driving the primary and secondary productivity cycles. This causes considerable spatial and temporal variability throughout the gulf in the biomass of the phytoplankton assemblage, its taxonomic composition and the abundance and biomass of the meso-zooplankton assemblages.

In NSG, there are several important spawning aggregation sites and nursery areas for Snapper (Fowler and Jennings 2003, Fowler et al. 2010). The spawning season extends from late November until late January with a significant peak in December (Chapter 3). This means that the Snapper eggs and larvae occur in the planktonic assemblage of NSG through until at least mid-February. Based on the study of Middleton et al. (2013) on the spatial and temporal plankton communities, there are several indications that this is an appropriate time for Snapper to reproduce so as to maximise larval survivorship. First, NSG supported the highest levels of biomass of phytoplankton for the entire gulf. Furthermore, in this northern region, the highest concentrations of chlorophyll *a* and the highest levels of biomass and abundance of meso-zooplankton were recorded in summer, corresponding with the Snapper reproductive season. With respect to zooplankton production in NSG, the biomass was low during November. However, by December, both the abundance and biomass had increased significantly and continued to do so reaching their maxima in February before declining in March and subsequently remaining low through winter. Therefore, the period of highest abundance and biomass of zooplankton in NSG corresponded to the spawning season of Snapper, thereby providing the best opportunity to minimise larval starvation. NSG was the only region of Spencer Gulf where zooplankton productivity displayed this pattern of seasonality.

During summer it appears that the environmental conditions in NSG are ideal for the spawning and recruitment of Snapper. There are appropriate spawning aggregation sites and nursery areas (Chapter 6). The early summer SSTs stimulate reproductive development and spawning by the adults (Chapter 3), and later are ideal for larval growth, development, and survivorship. The planktonic dynamics are such that the seasonality of phytoplankton and zooplankton abundances and biomass are highest during summer, providing the best conditions to minimise the risk of larval starvation.

7.4.4 Considerations about climate change

Snapper have an extensive distribution throughout Australasia. Throughout the many habitats they occupy they are exposed to a broad range of physical and biological environmental conditions. Nevertheless, across their latitudinal range, the timing of reproduction varies in a systematic way, i.e., the peak spawning times for populations at low latitudes (sub-tropical climates) is during winter, whereas for higher latitudes (temperate climates) it is during summer (Chapter 3). This means that the environmental conditions for when the eggs and larvae are delivered into the pelagic environment are relatively consistent across the different latitudes. Peak spawning times across the range tend to occur when the SSTs are between 18 and 22°C, i.e., the optimal range for the physiological development and survivorship of Snapper eggs and larvae.

For Snapper in South Australia, the main spawning grounds and nursery areas are located in NSG, and may well also be the case for NGSV. For both these regions, spawning by Snapper occurs between November and January (Chapter 3). For NSG, the summer SSTs throughout the 2000s have exceeded the optimal range of 18-22°C, whilst for NGSV it is likely that they are approaching this upper imit. Such elevated summer SST regimes may be compromising the natural reproduction/recruitment processes by impacting on the physiological development of the eggs and larvae. Future projected increases in SSTs may exclude the northern gulfs as suitable spawning areas during the spring/summer season (Pecl et al. 2014). Thus, high summer SSTs may have a major negative impact on recruitment and overall fishery productivity. This is the case since these regions support the important nursery areas from which other regions are eventually replenished through emigration (Chapter 10).

7.5 References

Bessell-Brown, P., Prosser, A., Garland, A. (2020). Pre-recruit abundance indices for Eastern King Prawn, Blue Swimmer Crab and Snapper in south eastern Queensland. Report to Fisheries Queensland, Department of Agriculture and Fisheries. 21 pp.

Cushing, D.H. (1988). The provident sea. Cambridge University Press. Pp 329.

Cushing, D.H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 29: 250-293.

Doherty, P., Fowler, A. (1994). Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. Bulletin of Marine Science 54: 297-313.

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

Fowler, A.J. (2000). Snapper (*Pagrus auratus*). Fishery Assessment Report to PIRSA for the MSF Fishery Management Committee. South Australian Fisheries Assessment Series 00/13. Pp 55.

Fowler, A.J. (2002). Snapper (*Pagrus auratus*). Fishery Assessment Report to PIRSA for the MSF Fishery Management Committee. South Australian Fisheries Assessment Series 01/013. Pp 65.

Fowler, A.J., 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., McGlennon. D. (2011). Variation in productivity of a key snapper, *Chrysophrys auratus*, fishery related to recruitment and fleet dynamics. Fisheries Management and Ecology 18: 411-423.

Fowler, A.J., McGarvey, R., Feenstra, J.E., Jackson, W.B., Jennings, P.R. (2003). Snapper (*Pagrus auratus*) Fishery. Fishery Assessment Report to PIRSA for the Marine Scalefish Fishery Management Committee. Pp 70.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E. Jackson, W.B. (2010). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-2, SARDI Research Report Series No. 473. Pp 109.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E., Jackson, W.B., Lloyd, M. (2013). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-3, SARDI Research Report Series No. 713. 103pp.

Fowler, A.J., McGarvey. R., Carroll, J., Feenstra, J.E., Jackson, W.B., Lloyd, M.T. (2016). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-4. SARDI Research Report Series No. 930. 82pp.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

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. (1995). Spatial and temporal 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., Langley, A.D., Gilbert, D.J. (1997). Prediction of snapper (*Pagrus auratus*) recruitment from sea surface temperature. In: Hancock, D.A., Smith, D.C., Grant, A., Beumer, J.P. (eds). Developing and sustaining world fisheries resources. The state of science and management. Second World Fisheries Congress. Melbourne, CSIRO Publishing. Pp 67-71.

Hamer, P., Conron, S. (2016). Snapper Stock Assessment 2016. Fisheries Victoria Science Report Series No. 10. Fisheries, Victoria, Queenscliff.

Hamer, P.A., 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., Acevedo, S. (2010). Importance of spawning in Port Phillip Bay to local snapper stocks. Fisheries Victoria Research Branch, No. 37, Queenscliff, Victoria.

Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 20: 1-228.

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. Fisheries Bulletin 87: 471-495.

Huang, B., Peter W. Thorne, et. al, 2017: Extended Reconstructed Sea Surface Temperature version 5 (ERSSTv5), Upgrades, validations, and intercomparisons. J. Climate, doi: 10.1175/JCLI-D-16-0836.1

McGarvey, R., Feenstra, J. (2004). Stock assessment models with graphical user interfaces for key South Australian marine finfish stocks. Final Report to FRDC (Project No. 1999/145). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 176 pp.

Middleton, J., Doubell, M., James, C., Luick, J., van Ruth, P. (2013). PIRSA Initiative II: carrying capacity of Spencer Gulf: hydrodynamic and geochemical measurement modelling and performance monitoring. Final Report to FRDC (Project No. 2009/046). South Australian Research and Development Institute (Aquatic sciences), Adelaide. SARDI Publication No. F2013/000311-1. SARDI Research Report Series No. 705. 97 pp.

Miller, T.J., Crowder, L.B., Rice, J.A., Marschall, E.A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45: 1657-1670.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2012). Interannual variation in larval survival of snapper (*Chrysophrys auratus*, Sparidae) is linked to diet breadth and prey availability. Canadian Journal of Fisheries and Aquatic Sciences 69: 1340-1351.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2013). Interannual variation in larval abundance and growth in snapper, *Chrysophrys auratus* Sparidae, is related to prey availability and temperature. linked to diet breadth and prey availability. Marine Ecology Progress Series 487: 151-162.

Pankhurst, P.M., Montgomery, J.C., 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.

Pecl, G., Ward, T., Briceño, F., Fowler, A., Stewart, F., Gardner, C., Hamer, P., Hartmann, K., Hartog, J., Hobday, A., Hoshino, E., Jennings, S., Le Bouhellec, B., Linnane, A., Marzloff, M., Mayfield, S., Mundy, C., Ogier, E., Sullivan, A., Tracey, S., Tuck, G., Wayte, S. (2014). Preparing fisheries for climate change. Identifying adaptation options for four key fisheries in south eastern Australia. Final Report to FRDC for Project 2011/039.

Saha, K., Zhao, X., Zhang, H., Casey, K., Zhang, D., Baker-Yeboah, S., Kilpatrick, K.A., Evans, R.H., Ryan, T., Relph, J.M. (2018). AVHRR Pathfinder version 5.3 level 3 collated (L3C) global 4km sea surface temperature for 1981-Present. NOAA National Centers for Environmental Information. Dataset. https://doi.org/10.7289/v52j68xx.

Saunders, R.J. (2009). The reproductive biology and recruitment dynamics of Snapper, *Chrysophrys auratus*. PhD thesis, University of Adelaide. 154 pp.

Saunders, R.J., Fowler, A.J., Gillanders, B.M. (2012). The spawning dynamics of snapper (*Chrysophrys auratus*) in northern Spencer Gulf, South Australia. New Zealand Journal of Marine and Freshwater Research 46: 491-510.

Sim-Smith, C.J., Jeffs, A.G., Radford, C.A. (2012). Variation in the growth of larval and juvenile snapper, *Chrysophrys auratus* (Sparidae). Marine and Freshwater Research 63: 1231-1243.

Sogard, S.M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60:1129-1157.

Sumpton, W., 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.

Zeldis, J.R., Oldman, J., Ballara, S., Richards, L.A. (2005). Physical fluxes, pelagic ecosystem structure, and larval fish survival in Hauraki Gulf, New Zealand. Canadian Journal of Fisheries and Aquatic Sciences 62: 593-610.

8. EARLY LIFE HISTORY CHARACTERISTICS FROM OTOLITH MICROSTRUCTURE

Anthony Fowler

8.1 Introduction

In South Australia, the dynamics in population size and temporal variation in size and age structures for Snapper populations are fundamentally driven by inter-annual variation in recruitment rates of the 0+ year class (Chapter 9, Fowler and McGlennon 2011, Fowler et al. 2020). For Snapper populations in Victoria and New Zealand also demonstrate temporal variability, year class strength is established very early in the life history (Zeldis et al. 2005, Murphy et al. 2012, 2013). To understand the population dynamics of Snapper it is necessary to understand the ecological aspects of the early life history. Whilst the different events, stages and processes of development that occur throughout the ontogeny of Snapper eggs and larvae, as well as their patterns of distribution and abundance were described in Chapters 4 and 5, further information on the ecology of these early stages came from the annual juvenile trawl surveys that were undertaken in Northern Spencer Gulf (NSG) between 2000 and 2010 (Chapter 6). Those surveys provided spatial and temporal information on the abundances of the 0+ and 1+ year classes. That study also provided specimens of 0+ Snapper whose earlier life history was revealed through the retrospective analysis of their otoliths. Whilst a preliminary analysis was provided for the juveniles captured during the first three years of the trawl survey, i.e., 2000, 2001 and 2002 by Fowler and Jennings (2003), the purpose of this chapter is to extend the comparison of the early life history characteristics to include all years of the survey from 2000 to 2010.

The results considered here were primarily from analysis of the microstructure of otoliths of juvenile Snapper (Fig. 8.1), interpreted based on a validation study that involved known-age juveniles, some that were tagged with tetracycline (Fowler and Jennings 2003). The validation trials demonstrated that the micro-increments in the otoliths of juvenile Snapper formed daily, with the first increment formed between the 2nd and 3rd days after hatching, corresponding to when exogenous feeding commenced. Furthermore, the otoliths of juvenile Snapper show a settlement mark that relates to when the fish settle from the plankton to the benthic environment. Based on the features of the microstructure of the otoliths of juvenile Snapper and when they form, the otoliths of the juvenile fish captured in otter trawl surveys between 2000 and 2010 provided estimates of age and pre-settlement duration. From this and the date-of-capture, it was possible to calculate the dates on which each fish was spawned, when it hatched from the egg and when it settled to the benthic habitat. The timing of these early life history events and processes for the successful recruits were compared amongst years and considered in the context of inter-annual environmental differences.

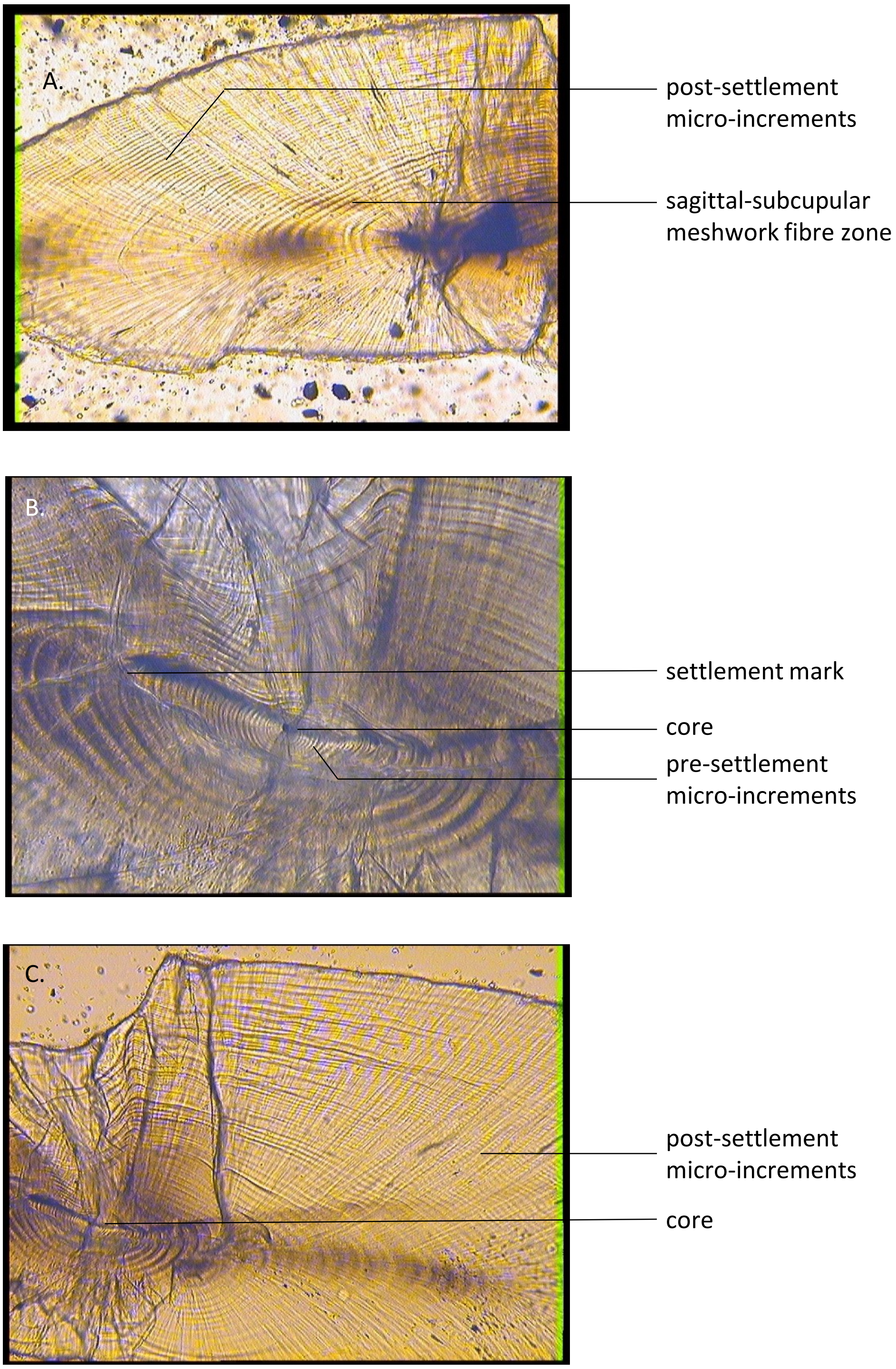


Fig. 8.1. Photomicrographs of the microstructure of the transverse sections of sagittae from juvenile Snapper sampled from NSG. A. Some pre-settlement and post-settlement micro-increments towards the ventral edge of the otolith. B. high-powered view of the primordium showing pre-settlement and post-settlement micro-increments. C. View of the proximal surface and part of the sulcus, showing the centrally-located core and some post-settlement micro-increments towards the ventral edge.

8.2 Materials and methods

The annual surveys for juvenile Snapper were undertaken between 2000 and 2010 throughout Northern Spencer Gulf (NSG) from the MRV *Ngerin* (Chapter 6). In April of each year, 10-minute trawl shots were done with an otter trawl at stations throughout the latitudinal zones from the Far Northern to Far Southern Zones (Fig. 8.2). The trawl catches were sorted on-board, and any 0+ Snapper captured were frozen and retained as such through to their return to the South Australian Aquatic Sciences Centre, and until they were processed.

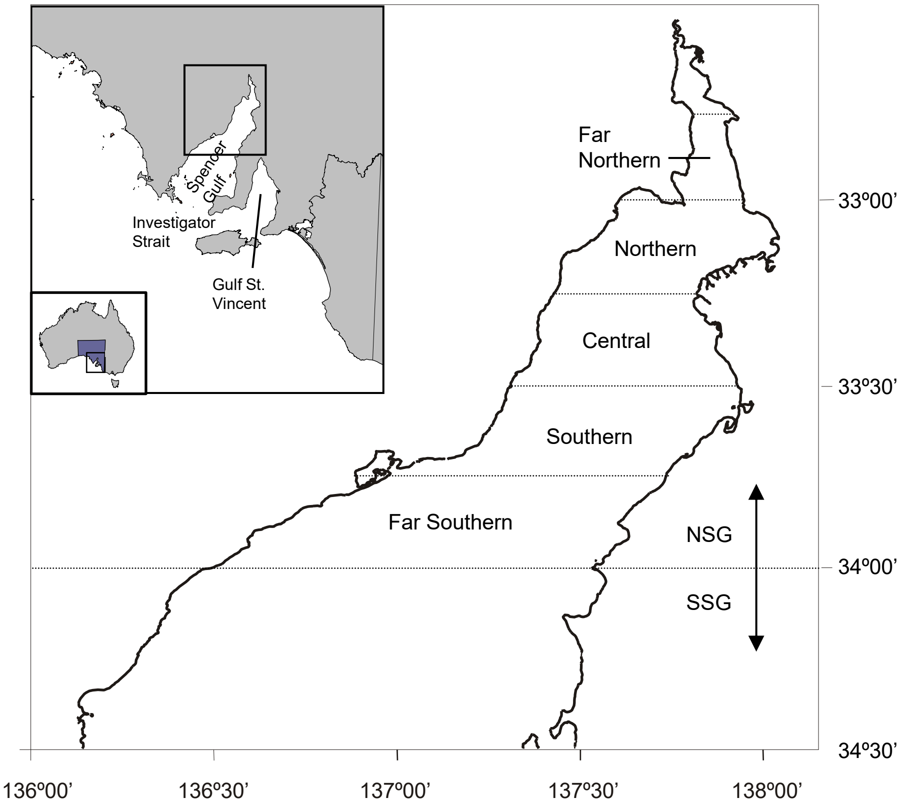


Fig. 8.2. Map of Northern Spencer Gulf showing five latitudinal zones in which sampling was done for juvenile Snapper from 2000 to 2010.

The juvenile Snapper captured in each year were processed in the months following the field trip. Each fish was measured (CFL), weighed (g) and dissected for removal of the sagittae, i.e., the largest pair of otoliths. For one sagitta from each fish, a transverse section was prepared as described in Fowler and Jennings (2003). The transverse otolith sections were examined and interpreted using a compound microscope at magnifications of x250 to 400, and an image analysis system. For each, the numbers of micro-increments from the primordium to the outside edge were counted along the dark band identified as the sagittal-subcupular meshwork fibre zone (Francis et al. 1992), i.e., the axis which generally provided the clearest complete sequence of micro-increments (Fig. 8.1). The total counts were differentiated into the pre-settlement and post-settlement components, based on the location of the settlement mark. The counts of micro-increments in association with fish size were used to calculate; age since hatch, pre-settlement duration, the dates when spawned and settled and the average growth rate. These biological parameters were compared amongst years and interpreted in the context of SST regimes for the different years. The SST data from satellite imagery were accessed from CSIRO. The data considered here were the average daily estimates of SST for the area of NSG, i.e., north of latitude 34°00’ (Fig. 8.2), for the period from 1st July 1999 to 30th June 2010.

Table 8.1. Summary of results from otter trawl surveys in April of each year from 2000 to 2010. For each reproduction/recruitment season the sampling period and number of 0+ Snapper captured are shown.

Season	Sampling period	No. 0+ Snapper
1999/2000	11-14 April 2000	67
2000/2001	4-7 April 2001	164
2001/2002	5-9 April 2002	8
2002/2003	12-13 April 2003	18
2003/2004	4-5 April 2004	36
2004/2005	22-23 April 2005	2
2005/2006	4-8 April 2006	254
2006/2007	11-13 April 2007	62
2007/2008	5-8 April 2008	3
2008/2009	17-18 April 2009	34
2009/2010	11-12 April 2010	144
Total		792

8.3 Results

8.3.1 Monthly estimates of SST

The trawl survey was done in April of each year from 2000 to 2010 (Table 8.1). The 0+ recruits captured had been spawned and their early ontogenetic development had occurred during the recent late spring and summer. To provide a coarse indication of the differences in SST regimes amongst years, the daily estimates of SST from July 1999 to June 2010 were used to calculate monthly averages (Fig. 8.3). The differences amongst years were least during winter and early spring but increased from October until at least February. In all years, SST increased from August up to at least January, and in some years to February, with the rate and scale of increase varying amongst years. Between November and February, which encompassed the period of reproduction, egg and larval development and settlement for Snapper (Chapters 3, 4, 5, 6), the monthly averages varied amongst years by up to 3°C. Such differences in SST regimes amongst years are likely to have been sufficient to impact reproduction and recruitment.

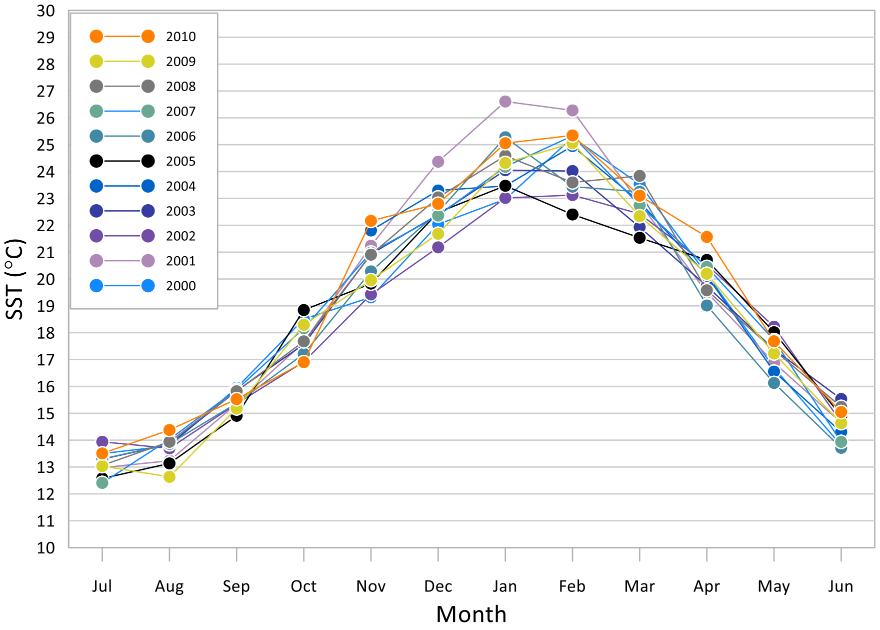


Fig. 8.3. Average monthly estimates of SST for NSG compared amongst the years from 2000 to 20010. Data obtained from satellite imagery.

8.3.2 Estimates of size and age

From 2000 to 2010, there were 792 0+ Snapper captured in the otter trawls (Table 8.1). Although there were differences in numbers of trawls done in different years, the differences amongst years in numbers of 0+ fish captured primarily related to variation in their density estimates (Chapter 6). A total of 754 fish were considered in the size and age analyses. The sizes of the 0+ fish captured across all years ranged from 21 – 106 mm CFL (Fig. 8.4a). The size distribution was multi-modal although most fish were in the 50 – 85 mm CFL size range. There was considerable variation in sizes amongst fish captured in different years, as evident for the five years that produced the highest numbers of 0+ recruits. Those taken in 2000 were evenly distributed from 21 to 98 mm CFL. For those taken in 2001, most were >50 mm CFL. The 2006-year class dominated the smaller sizes of <55 mm CFL, whilst those from the 2007 and 2010-year classes dominated the numbers of fish that were >60 mm CFL.

The differences in size distributions of the 0+ fish amongst years were related, in part, to differences in ages (Fig. 8.4b). A total of 721 fish were successfully aged, which ranged from 51 to 144 days post-hatch. The age distribution was multi-modal with the most abundant mode for the age range of 105 to 115 days of age, whilst the second most numerous mode was for the age range of 86 to 91 days. Fish older than 105 days were primarily captured in 2001, 2007 and 2010, whilst those younger than 91 days of age were dominated by those in the 2006-year class.

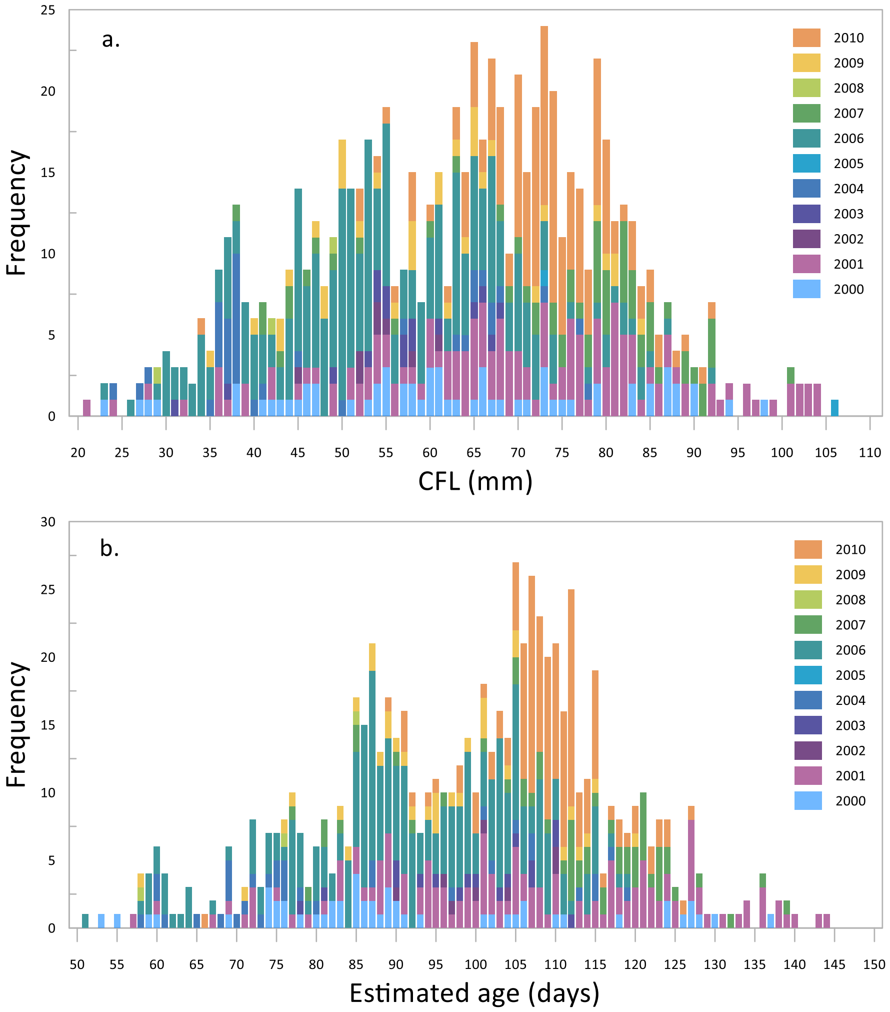


Fig. 8.4. Frequency distributions for the sizes and ages of 0+ Snapper captured during annual otter trawl surveys in NSG in April of each year between 2000 and 2010. a. sizes of juvenile Snapper. b. estimates of age for juvenile Snapper determined from otolith microstructure.

8.3.3 Pre-settlement duration

Being able to differentiate a settlement mark in the Snapper otoliths meant that the pre-settlement duration could be estimated. The estimates were normally distributed in the range of 15 to 30 days with most between 19 to 25 days (Fig. 8.5a). The median was 21 days, and the mean was 22.0 (±2.4 SD) days. The average estimates of pre-settlement duration varied considerably amongst years (Fig. 8.5b). The highest estimates were for juveniles collected in 2002, 2003 and 2004, whilst the lowest were for 2008 and 2009. For the five years that produced the highest numbers of successful recruits, the estimates of average pre-settlement duration were from 21 to 23 days.

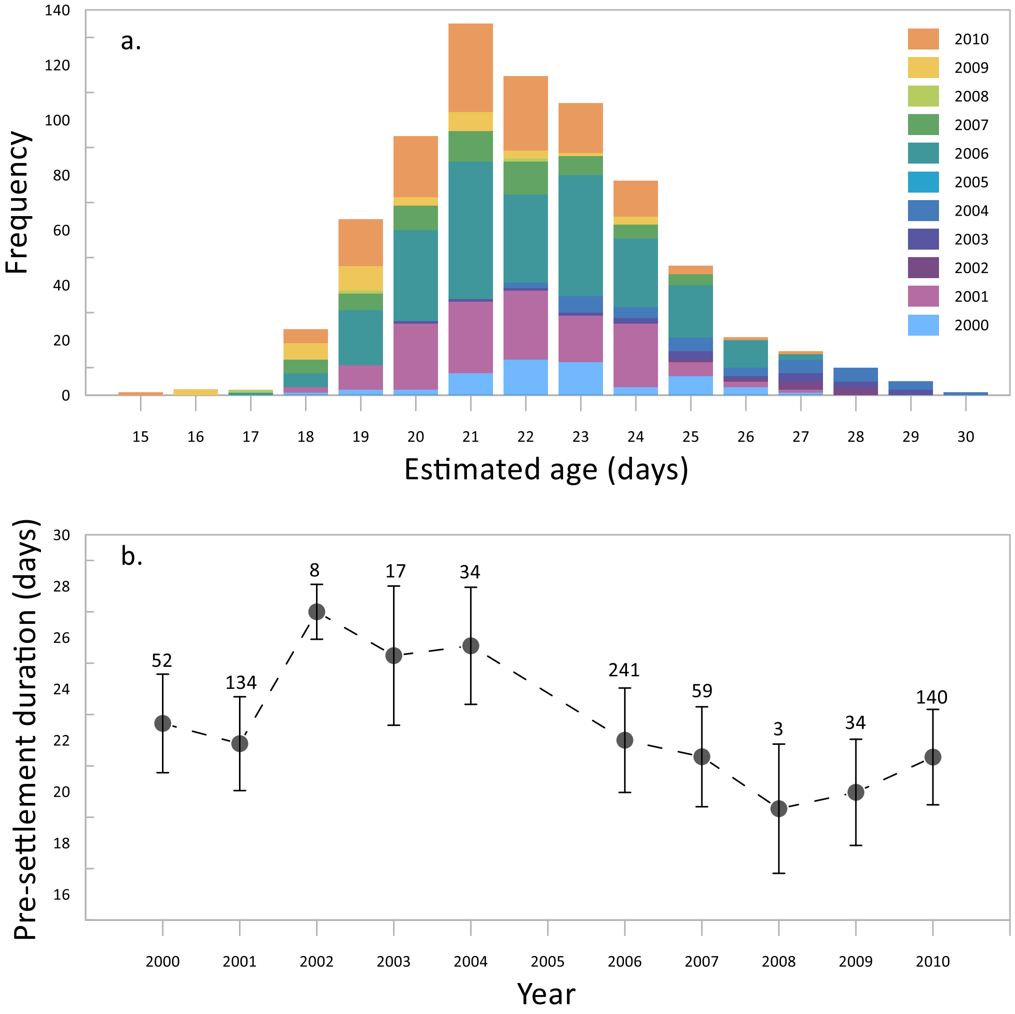


Fig. 8.5. Estimates of pre-settlement duration for the 0+ Snapper captured during annual otter trawl surveys in NSG in April of each year between 2000 and 2010. a. Frequency distribution. b. Estimates of annual average pre-settlement duration (±SD) (numbers show the sample size in each year).

Across all recruits sampled from 2000 to 2010, there was no relationship with the date of spawning (Fig. 8.6a). This was also the case for those years when the largest numbers of recruits were captured. There was also no relationship between the pre-settlement duration and the SSTs for the days on which the fish were spawned (Fig. 8.6b).

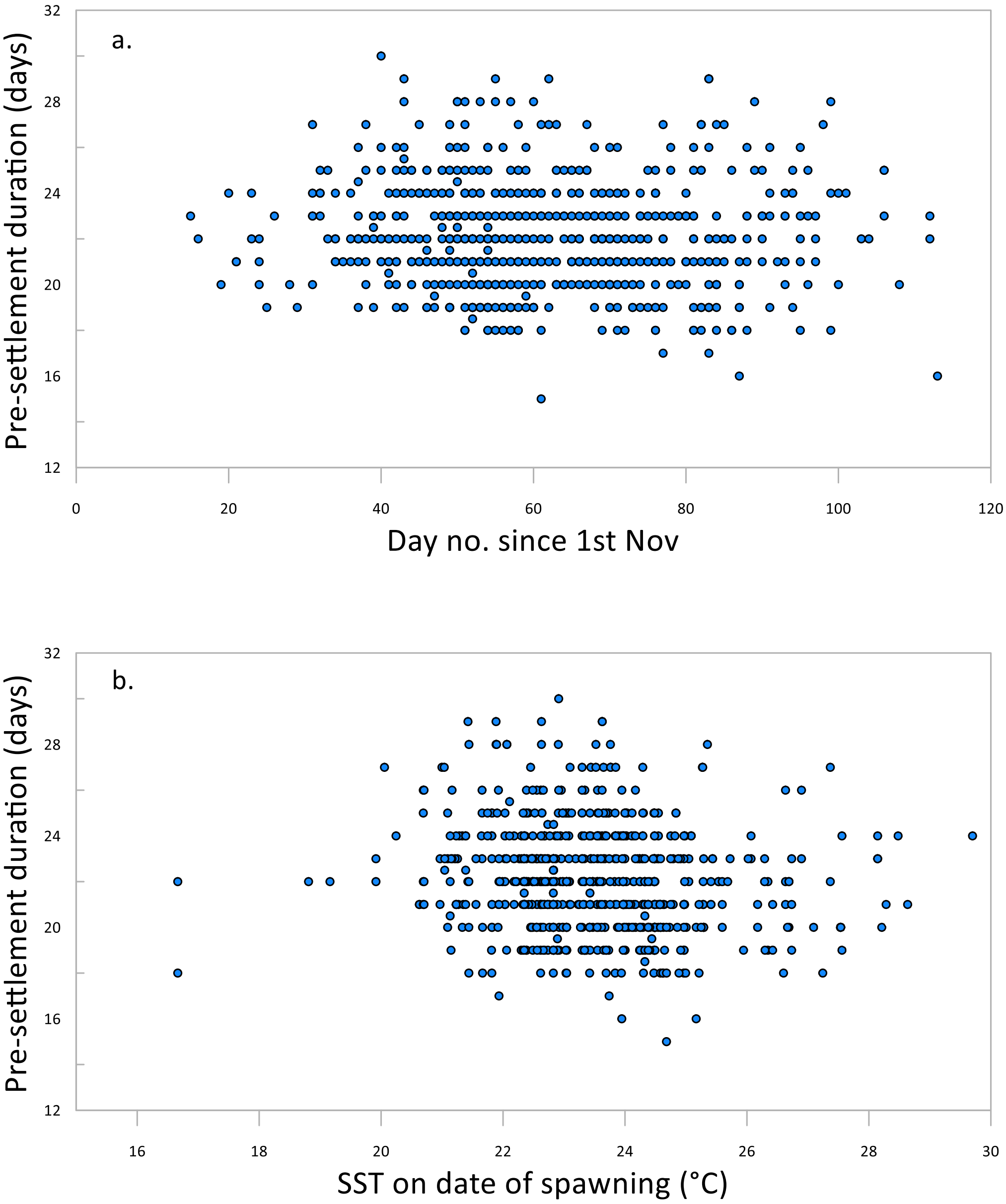


Fig. 8.6. Relationships for estimates of pre-settlement duration for 0+ Snapper captured during annual trawl surveys in NSG with external factors. a. relationship with the date of spawning in different years, as counted from the 1st November. b. relationship with the average SST on the day of spawning for each fish.

8.3.4 Estimates of SST, spawn dates and settlement dates

For all recruits across all years that were aged, the dates on which they were spawned were calculated. Most were spawned through December and January, although the rate was not uniform throughout this two-month period (Fig. 8.7a). Rather, the distribution was multi-modal with two modes in each of December and January that were approximately two weeks in duration. Furthermore, there was a broad range of daily SSTs on which successful recruits were spawned, nevertheless most originated on days when the SSTs were in the range of 22 to 25 °C (Fig. 8.7b). Within-year consideration of when successful recruits were spawned revealed that the successful spawn dates were grouped at certain times which differed amongst years (Appendix Fig. A8.1). In every year, the SSTs increased between September and January/ February, with the rate of increase and the timing of the maximum varying between years. However, the timing of spawning that ultimately led to successful recruitment consistently corresponded with when the SSTs increased through the range of 22-25°C (Appendix Fig. A8.1).

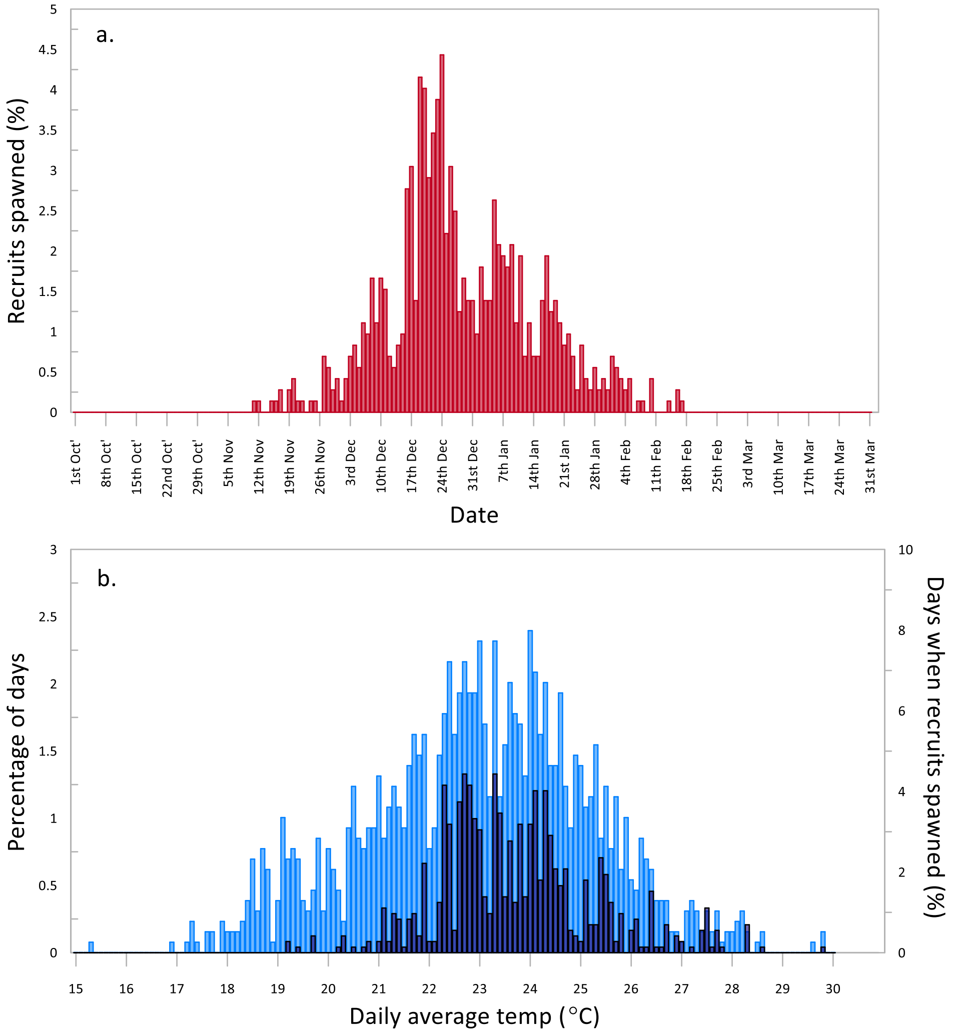


Fig. 8.7. Information on when recruits captured in otter trawls between 2000 and 2010 were spawned. a. Frequency distribution for dates on which recruits were spawned. b. Frequency distribution for SSTs of the days on which recruits were spawned (dark blue), and the number of days between November and February with nominated daily average SST (light blue).

The distributions of settlement dates of the successful recruits generally extended over weeks to several months, the timing of which varied amongst years (Fig. 8.8). For several years, there were multiple modes in these distributions, which varied in their timing and relative sizes, suggesting that throughout the reproductive/ recruitment seasons there were several waves of settlement. For the 1999/2000-year class, settlement occurred between December and early March, but was concentrated in early to mid-February 2000. For the 2000/2001-year class, the range in settlement dates was from early December until early March, but mostly occurred in December and January.

For the 2005/2006-year class, settlement was multi-modal with modes in early and late January as well as early and late February. For the bi-modal distribution in the 2006/2007-year class, settlement occurred predominantly in early January, with a smaller mode in early February. There was a single mode of settlement for 2009-2010 that occurred through mid-January.

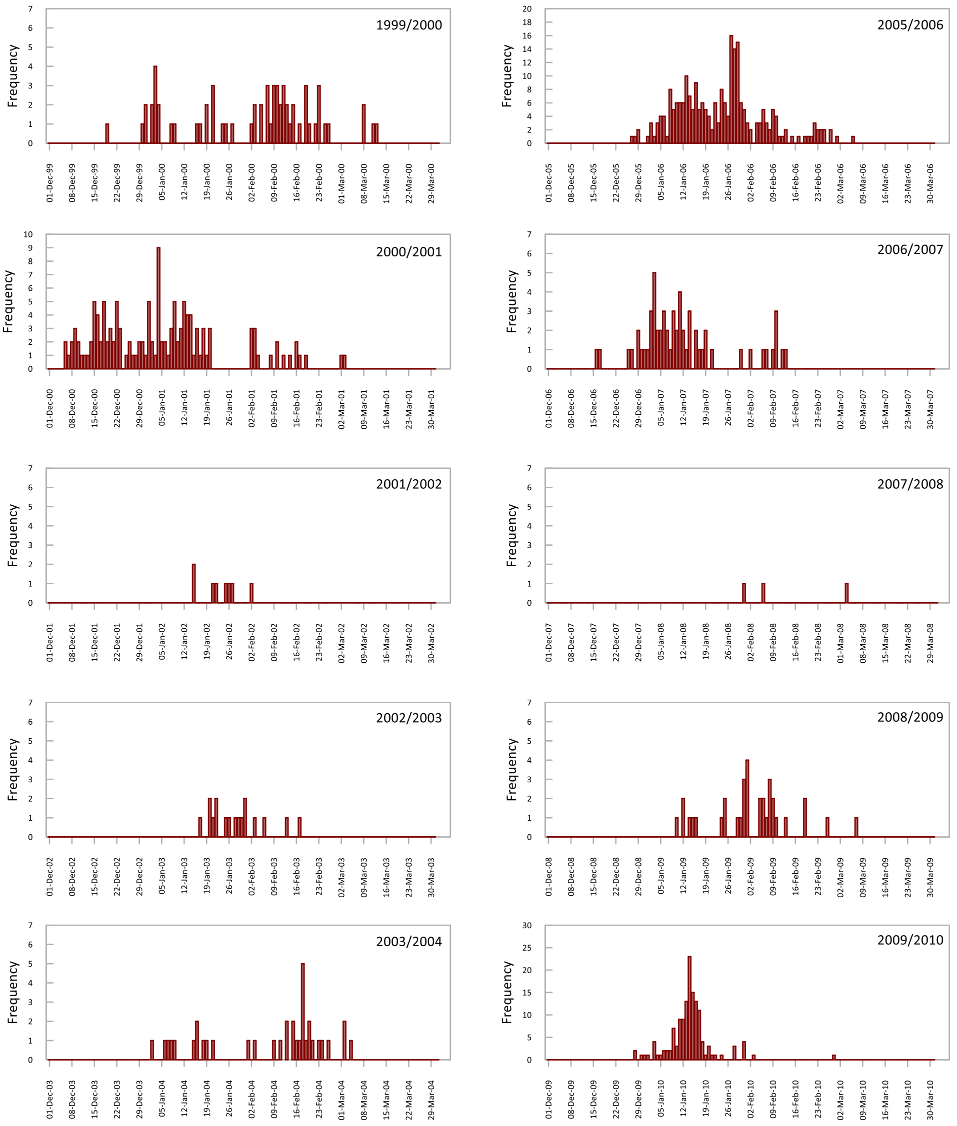


Fig. 8.8. Frequency distributions for estimated settlement dates for the 0+ Snapper captured during annual otter trawl surveys in April of each year between 2000 and 2010 in NSG.

8.3.5 Analysis of post-settlement growth

Instantaneous growth rates

For recruits sampled in all years there was a linear relationship for the estimates of size-at-age (CFL = (0.8936xAge) – 25.76), $p<0.001$, $r^2 = 0.8804$) (Fig. 8.9). The instantaneous growth rate was 0.89 $mm.day^{-1}$, whilst age accounted for 88% of the variation in fish size. For the individual years, the estimates of instantaneous growth rates were generally in the range of 0.8 – 0.9 $mm.day^{-1}$, although with two exceptions (Table 8.2, Fig. 8.10). For 2002, the growth rate was only 0.48 $mm.day^{-1}$. This particularly low growth rate might relate to the small number of fish sampled. Also, that year had the lowest estimates of SST for November, December and January of any year (Fig. 8.3, Appendix Fig. A8.1). In contrast, in 2007, the fastest growth rate amongst years of 0.99 $mm.day^{-1}$ was attained. The relatively similar growth rates amongst the other years mean that the differences in sizes of fish within and between years, as evident in Fig. 8.3a, were the consequence of when during the season that the fish were spawned and the period since settlement.

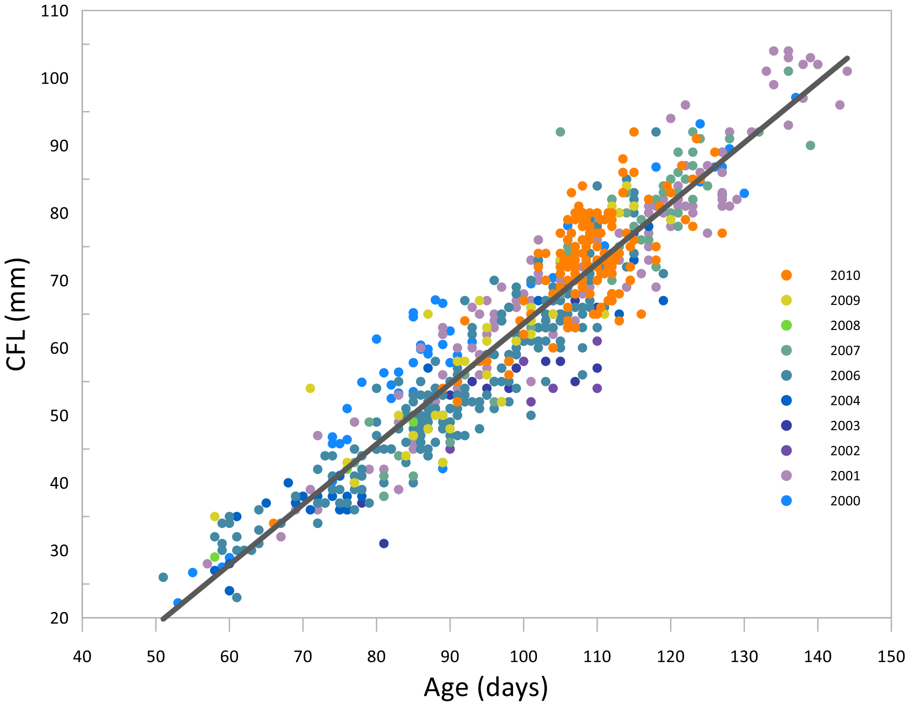


Fig. 8.9. Relationship of CFL against age for the recruits captured in all years differentiated by year of capture. The line shows the linear relationship for all data points.

Table 8.2. Summary of results of regression analyses for annual estimates of size and age for juvenile Snapper that were captured in annual otter trawl surveys and then successfully aged from their otoliths.

Season	Sample size	Equation	r^2
1999/2000	51	CFL = (0.823xAge) – 14.469	0.9128
2000/2001	134	CFL= (0.884xAge) – 23.878	0.9198
2001/2002	8	CFL = (0.482xAge) + 5.189	0.4180
2002/2003	17	CFL = (0.865xAge) – 30.010	0.7655
2003/2004	34	CFL = (0.801xAge) – 19.43	0.9359
2004/2005	2		
2005/2006	235	CFL = (0.869xAge) – 25.022	0.8621
2006/2007	59	CFL = (0.987xAge) – 35.283	0.8649
2007/2008	3		
2008/2009	34	CFL = (0.842xAge) – 20.332	0.7687
2009/2010	140	CFL = (0.810xAge) – 15.384	0.5513

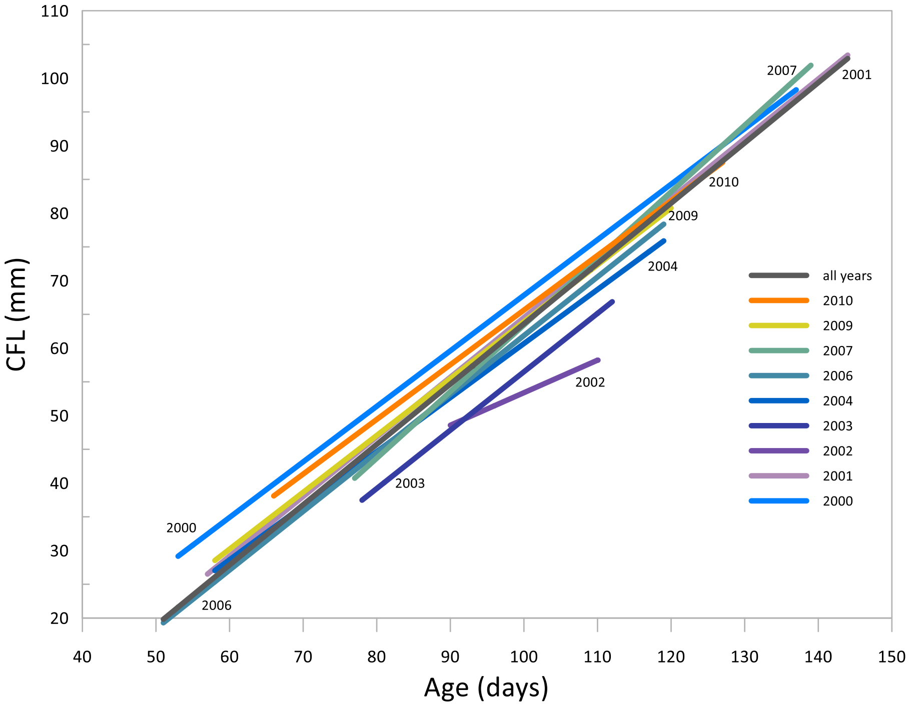


Fig. 8.10. Linear relationships between size and age for those years for which sufficient numbers of recruit Snapper were captured. The overall regression line through all data points is also indicated (black line).

8.4 Discussion

8.4.1 Background information

NSG is a highly significant region for the replenishment of South Australia's Snapper populations. It is the only coastal region for which significant nursery areas have been identified. It is now understood that not only do these nursery areas ensure that NSG is a self-recruiting region, but other regional populations such as SSG, SGSV and the West Coast of Eyre Peninsula are ultimately replenished from it (Chapter 11, Fowler et al. 2017). As such, its significance is comparable to that of Port Phillip Bay, for the Western Victorian Stock (Hamer et al. 2011). Analysis of population age structures (Chapter 9) and modelling with the fishery model SnapEst (Chapter 7) have provided some appreciation of the temporal variability in 0+ recruitment to NSG (Fowler and McGlennon 2011, Fowler et al. 2020). Over the past 50 years, the population dynamics and variability in fishery catches for the regional Snapper fisheries in Spencer Gulf have been primarily driven by only a few strong recruitment year classes (Chapter 9). The lack of such strong year classes through the 2000s has been a major contributor to the recent declines in these regional fisheries (Chapter 12, Fowler et al. 2020).

In 1999, a pilot survey for Snapper juveniles in NSG, indicated that otter trawling was a viable method for documenting spatial and temporal patterns of 0+ recruitment (Chapter 6, McGlennon pers. comm.). Based on this, in April of each year from 2000 to 2010, an annual otter trawl survey was undertaken that was aimed at providing an annual index of recruitment as a relative indicator of future fishery catches, and to provide some understanding of the inter-annual variability in recruitment. This was addressed through two objectives: to describe the spatial and temporal patterns in recruitment of the 0+ fish in NSG; and to elucidate aspects of the early life history and larval and juvenile ecology towards understanding the processes that regulate recruitment. This chapter has focused on the latter objective. The otter trawls provided specimens of juvenile Snapper whose earlier life histories were elucidated from the microstructure of their otoliths. Previous work had identified the relationship between the characteristics and development of otoliths of juvenile Snapper and the events and processes experienced by the larval and juvenile fish throughout their life histories (Francis et al. 1992, Fowler and Jennings 2003). Those studies demonstrated that the micro-increments in otoliths were formed daily from the day of first feeding onwards and that a settlement mark differentiated the micro-increments into those that formed during the pre-settlement and post-settlement phases. These characteristics meant that for those 0+ Snapper that were captured between 2000 and 2010 and successfully aged, the following variables could be estimated: total age since hatch; the pre-settlement duration; growth rate; and the dates on which it was spawned, hatched, and eventually settled to the benthic environment.

8.4.2 Early life history processes

Estimates of pre-settlement duration

Between 2000 and 2010, a total of 792 0+ Snapper were captured in NSG. The numbers varied amongst years, as related to their densities in the nursery areas. They ranged in size from 21 to 106 mm CFL, whilst their ages ranged from 51 to 144 days post-hatch. Besides the numbers, there was considerable variation in the size and age distributions amongst the different years. The ages included the estimates of pre-settlement duration, which ranged from 15 to 30 days, with a mean of 22 days. These statistics on pre-settlement duration for NSG are similar to those that were reported earlier based on sampling in fewer years and smaller sample sizes (Fowler and Jennings 2003, Saunders 2009). For NSG, there were differences amongst years in the estimates of pre-settlement duration. However, these differences were apparently not related either to the dates on which the fish were spawned or the SSTs for the dates on which they were spawned. This suggests that some factor(s) other than SST determined the pre-settlement durations, i.e., the periods between hatching and settlement. Snapper from the Hauraki Gulf, New Zealand, during the 1990s displayed similar overall statistics for the estimates of pre-settlement durations to those for Snapper from NSG, and also displayed differences amongst years. In that case, there were significant relationships between the estimates of pre-settlement duration and SST and the dates on which successful recruits were spawned. This difference between the Hauraki Gulf and NSG may relate to the difference in the durations of their spawning seasons (see below).

Timing of successful spawning

For NSG, the development of the gonads for the up-coming reproductive season commences in September and October (Chapter 3). Spawning commences in November, with peak spawning in December, followed by a decline in January, with only equivocal evidence that spawning continues into February (Saunders 2009). Between 2000 and 2010, the dates on which the successful recruits to NSG were spawned corresponded to the peak spawning months of December and January. Only for the 2000/2001 season was there a substantial mode of recruitment that originated in mid-to-late November. The successful spawn dates across years were late when compared to other jurisdictions, reflecting the compressed spawning season for Snapper in NSG (Chapter 3). For the Hauraki Gulf, New Zealand, the first successful spawn dates varied amongst several consecutive years but were as early as mid-September (Francis 1994). For PPB, Victoria, the hatch dates for juveniles that were captured after each spawning season between 2000 and 2011 were estimated. These ranged from late October until late February but were dominated by fish that were spawned throughout November and declined consistently from late November until February (Hamer pers. comm.). Furthermore, for Cockburn Sound, Western Australia, another important spawning site and nursery area for Snapper in southern Australia, spawning occurs between September and January (Wakefield 2010). Thus, compared with other jurisdictions in southern Australia and New Zealand, the spawning season in NSG is considerably compressed in duration. This means that there is limited time available for the spawning stock to generate a significant cohort of successful recruits. The limited duration of the spawning season probably accounts for the lack of relationships between pre-settlement duration with spawn date and SST that are evident for other jurisdictions.

The compressed reproductive season in NSG compared to other southern, temperate jurisdictions in Australia and New Zealand may relate to the influence of different SST regimes on the physiological maturation of the adult Snapper. For example, even amongst the regions of Spencer Gulf and Gulf St. Vincent (NSG, SSG, NGSV, SGSV), there are differences in the duration of the spawning seasons (Chapter 3). Because of its geography, NSG is characterised by having a broad range in seasonal SSTs, between high summer SSTs and low winter temperatures (Nunes and Lennon 1986). For those years considered in this study, the range in monthly average estimates of SST for NSG was from 12.4 to 26.6°C. Similarly, NGSV also experiences a broad range in seasonal water temperatures and has a compressed spawning season. In comparison, the southern gulfs display lower seasonal ranges in SSTs but have more extended spawning seasons (Chapter 3). It is difficult to compare reported SST regimes between different places, as they have likely been recorded at different spatial scales and places in the water column. Nevertheless, it appears that Port Phillip Bay, Cockburn Sound and the Hauraki Gulf, which all have reproductive seasons that are longer than those in NSG by several months, do not experience the same seasonal extremes in SST (Chapter 3).

For NSG, there was considerable variation in the rates of increase and the timing of increase in SST during the spring and summer. Furthermore, the timing of the ‘windows of opportunity’ that produced successful recruitment also varied amongst seasons. However, most recruits captured, regardless of which year, were spawned when the SSTs increased through the range of 22-25°C. This implies the possible influence of physiological tolerance limits on the survival and development of the Snapper eggs and larvae. Laboratory rearing experiments for Snapper eggs and larvae have demonstrated optimal temperature ranges for development and survival for both stages (Chapters 3, 7). For the development and survival of the eggs of *Pagrus major*, the optimal temperature range was 15 - 22°C (Mihelakakis and Yoshimatsu 1998). Furthermore, in a larval rearing experiment that involved water temperatures of 15, 18, 21, 24, 27, 30 and 33°C, mortalities of larvae were 100% in the temperature treatments of 27°C and greater (Fielder et al. 2005). It is difficult to relate the upper physiological temperature limit identified in a tank experiment when temperatures are held constant, with those likely to be experienced by the larvae in a large water body such as NSG. Nevertheless, the upper physiological limit identified experimentally was similar to the maxima attained in NSG during summer.

As indicated above, the production of successful recruits in NSG in different years corresponded with the SST range of 22-25°C. However, this was not a sufficient condition to ensure successful recruitment. For example, throughout most of December 2004 and January 2005, the SSTs were in the optimal range, yet no successful recruits were recorded from spawning during this season. Similarly, throughout most of November and December 2007, the SSTs were in the optimal range, but only three recruits were captured in April 2008. Other studies on early life history development and recruitment variability for Snapper have identified the influence of factors other than SST (Zeldis et al. 2005, Murphy et al. 2012, 2013). In both the Hauraki Gulf and Port Phillip Bay, inter-annual variation in numbers and survivorship of post-yolk sac Snapper larvae were related to the plankton dynamics (Chapter 7). The latter influenced the diets of the developing Snapper larvae and ultimately affected their survivorship. This indicates that even if SSTs are in the optimal range for larval development and survivorship, there are also significant ecological influences that also affect survivorship.

8.5 References

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

Fowler, A.J., 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., McGlennon, D. (2011). Variation in productivity of a key snapper, *Chrysophrys auratus*, fishery related to recruitment and fleet dynamics. Fisheries Management and Ecology 18: 41-423.

Fowler, A.J., Hamer, P.J., Kemp, J. (2017). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely-dispersed, coastal fishery species. Fisheries Research 189: 77-94.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

Francis, M.P. (1994). 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., Williams, M.W., Pryce, A.C., Pollard, S., Scott, S.G. (1992). Daily increments in otoliths of juvenile Snapper, *Pagrus auratus* (Sparidae). Australian Journal of Marine and Freshwater Research 43: 1015-1032.

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Mihelakakis, A., 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.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2012). Interannual variation in larval survival of snapper (*Chrysophrys auratus*, Sparidae) is linked to diet breadth and prey availability. Canadian Journal of Fisheries and Aquatic Sciences 69: 1340-1351.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2013). Interannual variation in larval abundance and growth in snapper *Chrysophrys auratus* is related to prey availability and temperature. Marine Ecology Progress Series 487: 151-162.

Nunes, R.A., 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.

Saunders, R.J. (2009). The reproductive biology and recruitment dynamics of Snapper, *Chrysophrys auratus*. PhD. Thesis, University of Adelaide, Adelaide, South Australia. 154 pp.

Wakefield, C.B. (2010). Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. Journal of Fish Biology 77: 1359-1378.

Zeldis, J.R., Oldman, J., Ballara, S.L., Tichards, L.A. (2005). Physical fluxes, pelagic ecosystem structure and larval fish survival in Hauraki Gulf, New Zealand. Canadian Journal of Fisheries and Aquatic Sciences 62: 593-610.

8.6 Appendices

8.6.1 Annual patterns of SST and timing of successful spawning

For the 1999/00 season, SST increased above the long-term average during August, September and October, but declined in late October (Fig. A8.1). Through November, December and January, SSTs were generally below average, before increasing in late February and early March. There were several modes in the dates on which the successful recruits were spawned. The range in the timing was from late November to mid-February, corresponding to the period during which SST ranged from 22 to 25°C.

For 2000/01, through August, September, October until mid-November, the SSTs were similar to the long-term average (Fig. A8.1). In mid-November, the SSTs increased rapidly by a few degrees, and then remained above average by several degrees until mid-March. This season produced the second highest number of recruits. There were several modes of spawn dates, i.e., during mid-November, early, mid- and late December, and early January. The first mode was the earliest of any across all eleven years. The spawn dates primarily corresponded to the SST range of 22-25°C. When SST exceeded 25°C in early January, there was a considerable decline in numbers of successful recruits that were spawned.

In the season of 2001/02, the summer SSTs were generally cool, i.e., below average from October until mid-March (Fig. A8.1). Only eight successful recruits were captured in this year. These were spawned in mid-late December when SSTs increased to 21°C and then to 22°C. Further increases in SST up to 24°C in January did not lead to a continuation in successful spawning.

In 2002/03, the SST regime largely conformed to the long-term averages apart from a minor decline in late December to mid-January (Fig. A8.1). Also, from mid-February until mid-April, the SSTs were marginally below average. Only 17 recruits were captured that were spawned between late December and mid-January. They corresponded with the timing in the increase in SST above 22°C but remained below 25°C.

In 2003/04, there were no SST data available until late November. From December to March, the SSTs were variable (Fig. A8.1). Through December they were above average, but in early January fell below average before increasing again in February. There were two apparent peaks in recruitment, one throughout December and the second in mid-January to early February. Both modes corresponded with SSTs of 22-25°C.

For 2004/05, some estimates of SST during October were not available. Largely through September, November, January and February, the SSTs were below average but in December they were approximately near average (Fig. A8.1). Only two recruits were captured in this season.

Neither was aged, and so the spawn dates were not available. This means that the long period between mid-November and early March during which the SSTs were between approximately 22 and 23°C, produced very few recruits.

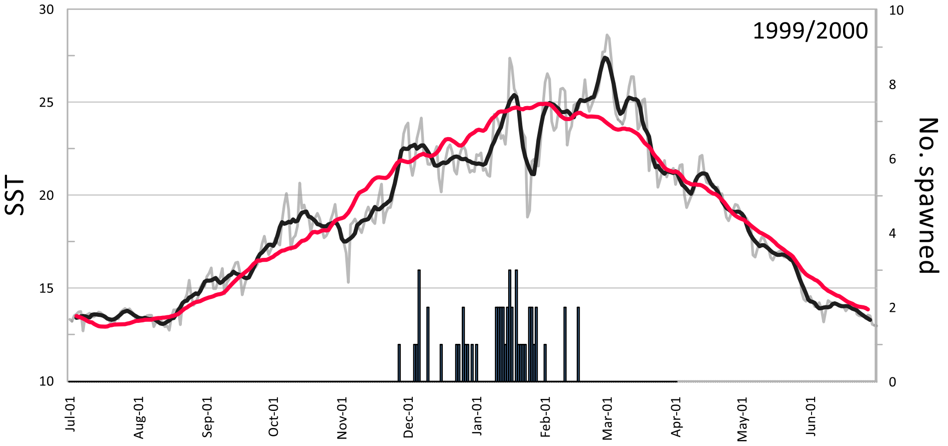
The SSTs in 2005/06 largely conformed to the long-term averages until January, when they increased above this level (Fig. A8.1). However, in late January they decreased and subsequently remained below the long-term average line throughout February. This season produced the highest numbers of recruits. Their spawn dates were multi-modal and were primarily throughout December and January, which corresponded with a long period of increasing SST from 22-25°C. For a period when SST exceeded 25°C, there was a decline in the numbers of successful recruits spawned. As the SST fell below 25°C, the numbers increased to another small peak.

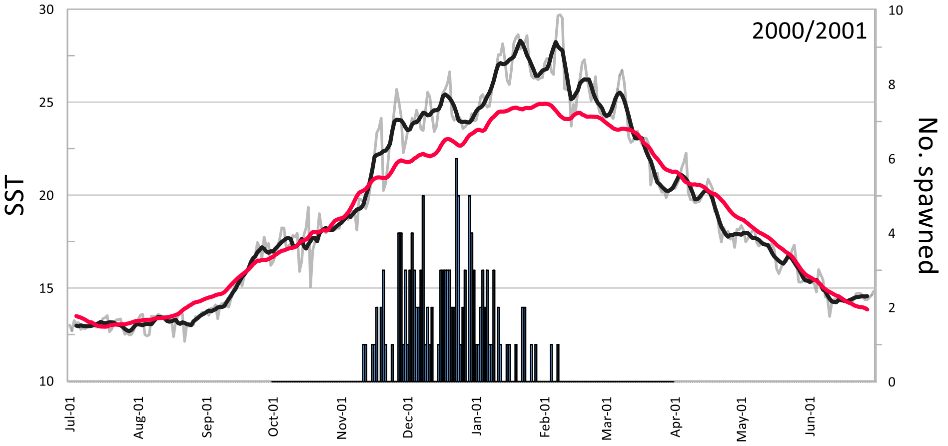
Through 2006/07, the trends in SSTs largely conformed to the long-term averages, although they were quite variable regularly increasing above and then declining below the averages line (Fig. A8.1). The fewer recruits captured for this season were primarily spawned during December as SST increased from 20°C to 24°C. The second minor peak in mid-January corresponded with SSTs of 23-24°C.

Throughout 2007/08, the SSTs were again quite variable oscillating around the long-term average line (Fig. A8.1). There were only three recruits captured that were spawned between mid-January and early February, when the SST was approximately 24°C. This was the only year for which there were no successful recruits that were spawned in either November or December, despite there being numerous days when the SST was between 22 and 24°C.

The SSTs in 2008/09 were more stable than in previous years and largely conformed to the average line until late January – early February, when they increased quickly by several degrees before declining back to the average line (Fig. A8.1). The single peak in successful spawning occurred between late December and late January, when the SSTs increased from 22 to 25°C.

In 2009/10, the SSTs were again variable, but largely conformed to the long-term average line (Fig. A8.1). In November, the SSTs increased above the long-term average by several degrees before declining again. For the relatively large number of recruits captured in 2010, the spawn dates formed a unimodal distribution with the highest frequencies associated with a number of days in mid-late December. This mode corresponded to increasing temperatures from 21 to 24°C.





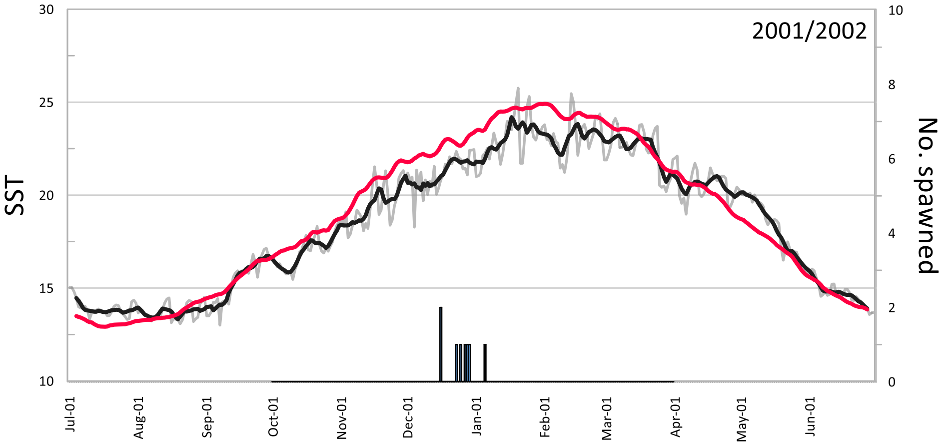
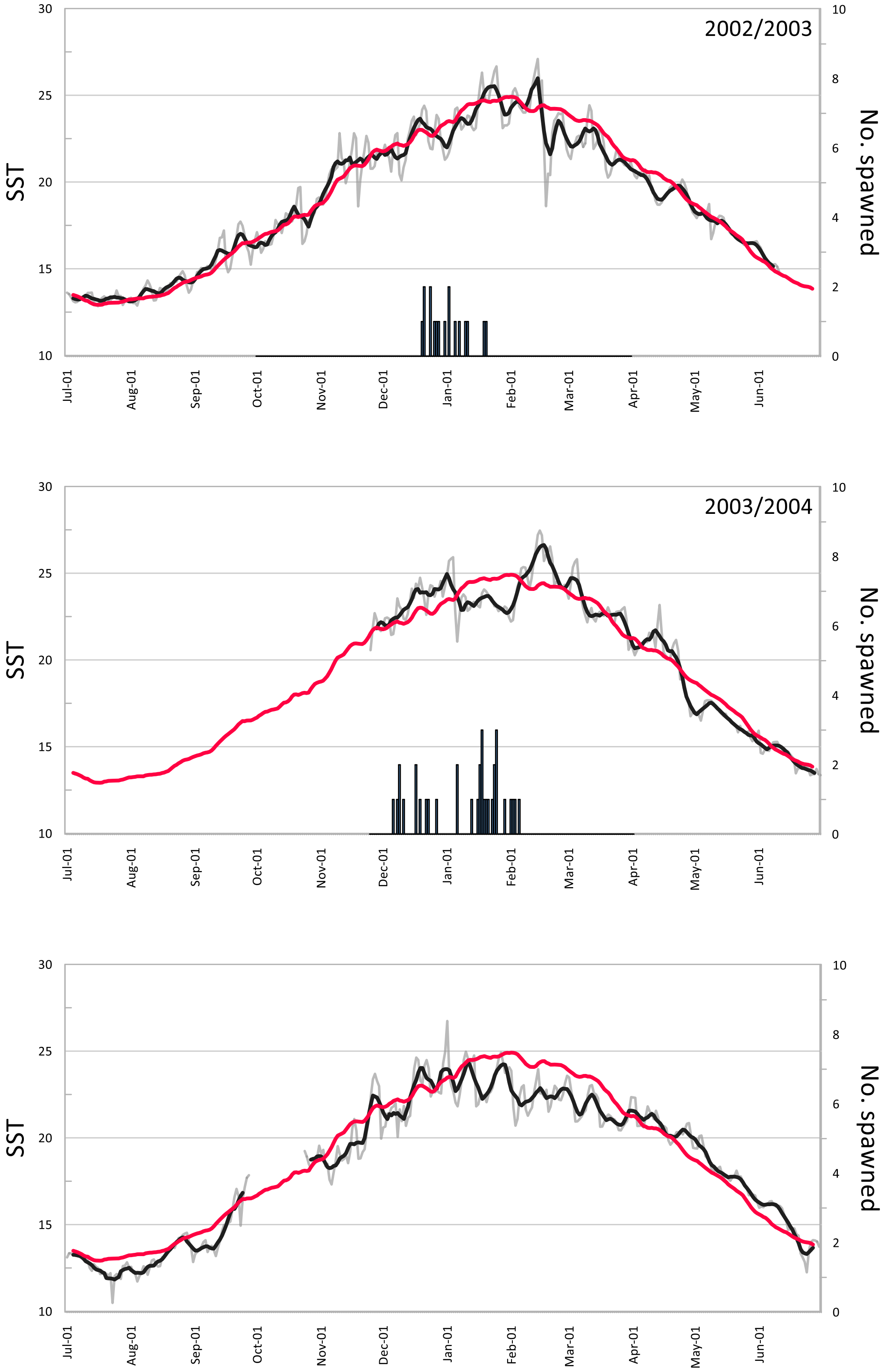


Fig. A8.1. Summary of SST data for NSG from satellite imagery. Data for each year show the daily averages (grey line), the 7-day running average (black line), and the long-term average of the 7-day running averages between 1999 and 2010 (red line). Bar chart shows the number of captured recruits spawned each day.



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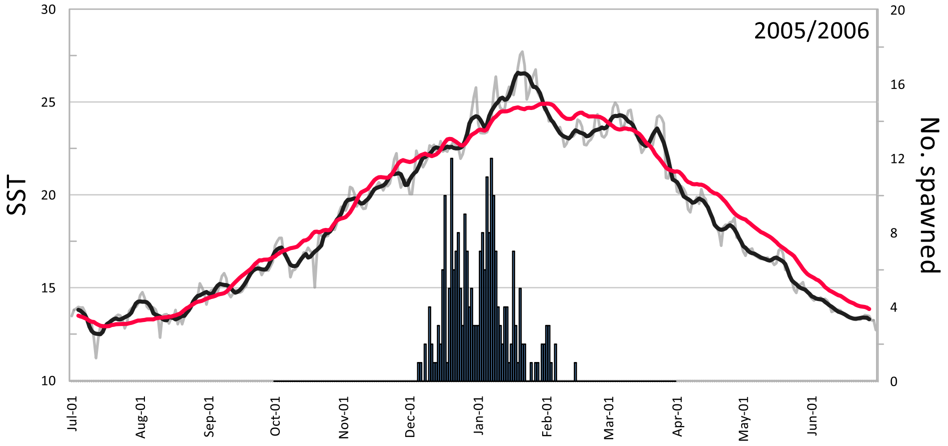

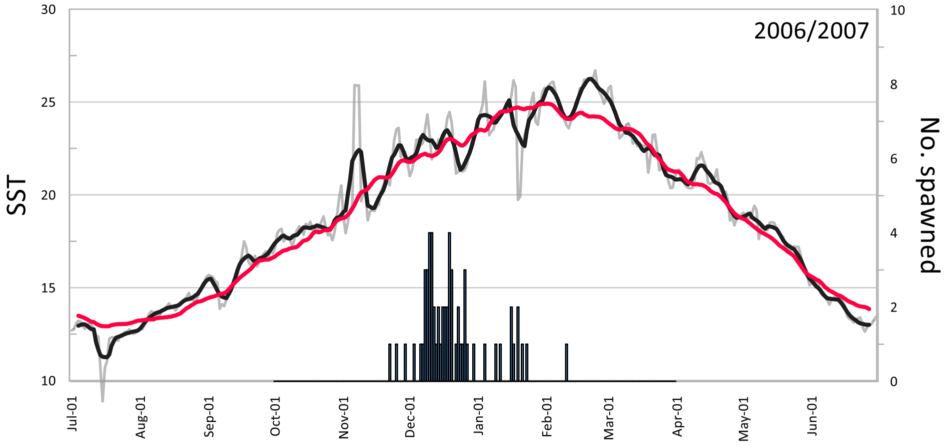

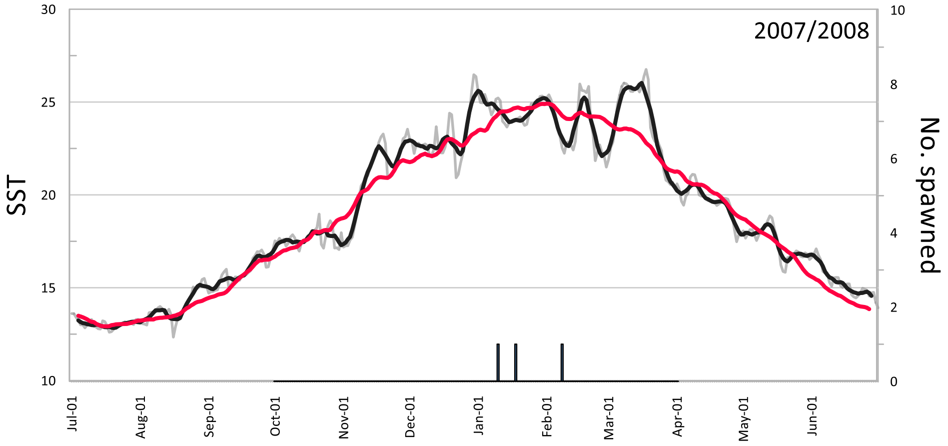

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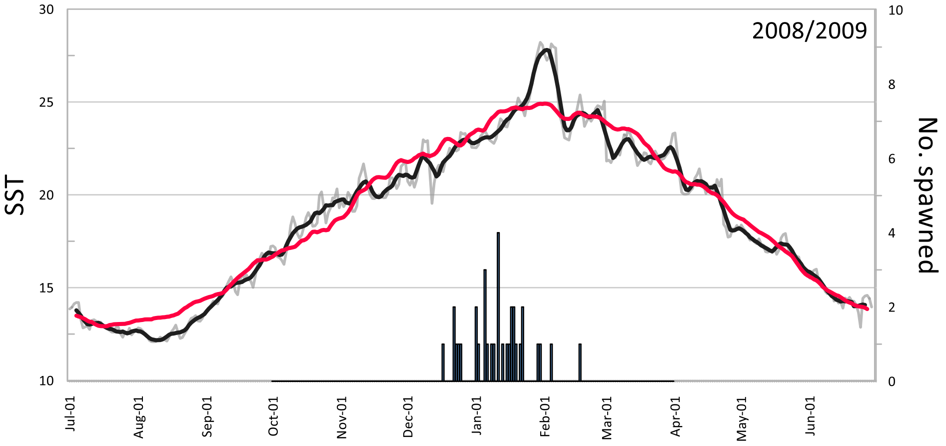

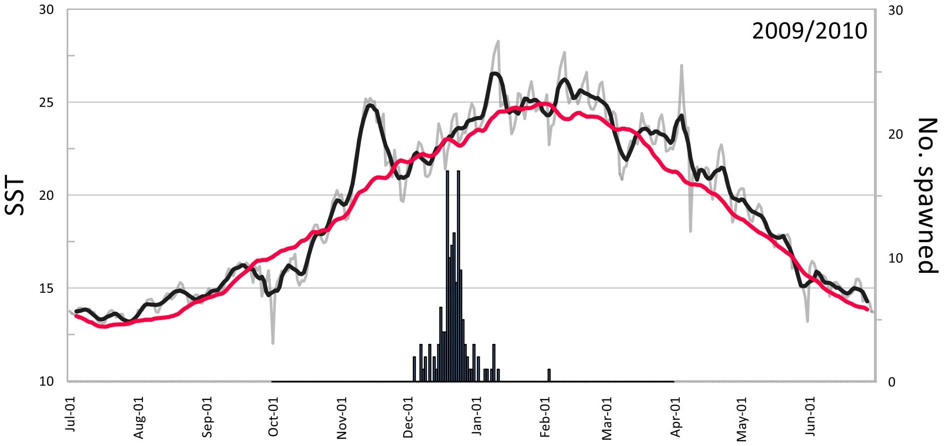

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9. ESTIMATING AGE AND AGE-RELATED POPULATION PARAMETERS

Anthony Fowler

9.1 Introduction

For studies that focus on the population biology of fish species, estimates of fish age constitute one of the most significant and influential biological variables (Campana 2001, Campana and Thorrold 2001). Such estimates provide the fundamental information for understanding the demography and life history of the fish species and for assessing the productivity of its fishery. Estimates of fish age constitute the measures of elapsed time that allow the calculation of rates of demographic processes such as growth and mortality. Furthermore, significant population processes such as reproduction, recruitment and movement can be related to age (Fowler 2009). There are three techniques for estimating fish age: length frequency analyses, tag-recapture studies, and direct ageing from hard anatomical structures. Of these, the latter is least prone to subjective interpretation and tagging artefacts (Brothers 1982). As a result, the direct ageing of fish from their hard, bony structures and its application to fishery science and management constitutes the most significant application of ageing in natural resource management (Campana 2001).

Despite the extensive scientific effort that goes into direct ageing of fish at marine research facilities on an annual basis around the world and its significance to fish population studies and fishery management, the process of determining fish age in years is still subject to several possible sources of error that can result in erroneous estimates of fish age (Campana 2001). If undetected, such errors would be propagated through the subsequent quantitative processes resulting in incorrect age structures, erroneous estimates of growth rates, mortality rates, yield estimates and understanding of the potential productivity of the fishery (Lai and Gunderson 1987, McFarlane and Beamish 1995, Eklund et al. 2000). As such, fish biologists need to be aware of these issues and to mitigate against their influence. There are two major sources of error. ‘Process’ error can occur from the choice of the bony structure that is used for direct ageing and result from the lack of appropriate consideration of validation processes. Not all bony structures of fish form a complete growth record throughout the lifetime of the animal and even for structures that do show a complete record, this may not occur along all growth axes. ‘Process’ errors commonly occurred prior to the 1980s when the ageing of fish was based on interpretation of the structure of their scales or whole otoliths, which resulted in age estimates that under-estimated the true ages (Power 1978). For fish, the development of an ageing protocol based on direct ageing from a hard, bony structure, there must be attention to appropriate validation processes.

Fish otoliths have emerged as the hard structure of choice for direct ageing studies for many fish species around the world. Nevertheless, even when an ageing methodology involving otoliths has been validated and their growth and structure are understood, it is inevitable that ageing errors will still occur (Campana 2001, Morison et al. 2005). This relates to the fact that the macrostructure of otoliths is complex, displaying a variety of increments and discontinuities, which can vary in clarity and interpretability both amongst individuals and amongst populations from different places (Fowler 2009). As such, errors can be made when interpreting otolith structure (Campana 2001, Morison et al. 2005). The correct interpretation of such complex structures is a skill that must be learned and practised, for which there is considerable variation in aptitude amongst different personnel (Morison et al. 2005). So, the monitoring of consistency in fish ageing work requires implementing appropriate quality assurance (QA) and control (QC) procedures. QA covers procedural matters that are generally applied laboratory-wide such as staff training, procedure manuals, calibration, instrument maintenance and review (Morison et al. 2005). This, for example, would involve the monitoring of consistency in ageing work to ensure that fish ageing does not drift over time. QC relates to the processes that are used to check results from fish ageing work, the assessment of repeatability and or precision of age estimates. These include the use of age-bias plots and measures of precision and repeatability as quantitative measures that allow appropriate comparisons for individual readers over time and between otolith readers (Campana 2001, Fowler 2009).

The purpose of this chapter is to provide a synthesis of the fish ageing studies that have been done for Snapper in South Australia. There have been different periods through the research history of Snapper across which the fish ageing protocol and QA/QC procedures have evolved. For the different stages through this history, the information that is considered below includes: a description of the fish ageing protocol, the considerations that were paid towards validation and QA/QC processes and the results in terms of fish age and age-based parameters. This chapter also provides a summary of the age-related information that has been collected throughout the 2000s for the regional populations of South Australia.

9.2 Materials and methods

9.2.1 Chronology of ageing studies

For this review, historical reports, theses, and publications from the 1980s to the 2000s were considered. Details in relation to the different ageing methodologies and the consideration towards QA/QC procedures were gleaned and summarised.

9.2.2 Population age structures 2000 – 2020

Since 2000, a biological research program has been undertaken for Snapper in South Australia. This has involved market sampling for Snapper captured by commercial fishers in the Marine Scalefish Fishery. Such sampling has been concentrated at the SAFCOL fish market, but occasionally involved catches that were accessed at other processors or from particular fishers. These commercial catches were also augmented by catches that were taken on research field trips (Fowler et al. 2020). Due to the closure of South Australia's Snapper fisheries in November 2019, an alternative form of adult sampling has been used to access samples to provide information on fish size and age, i.e., commercial fishers have been contracted by SARDI to target and to provide samples of Snapper.

The commercial catches landed at various ports around Gulf St. Vincent and Spencer Gulf were trucked overnight to the SAFCOL market, to be auctioned early the next morning. Generally, once per week, prior to the morning auction, a research team processed catches of Snapper. The catches processed were selected from those available to ensure as broad a geographic coverage as possible. A two-stage sampling protocol was used. First, as many fish as possible from each chosen catch were measured. Subsequently, a subset of fish was processed for the collection of otoliths, to be used later for age determination. Subsequently, these fish were measured for CFL, weighed, gutted, and their sex and stage of reproductive development were determined. Later, in the laboratory, one otolith from each fish was embedded in resin and sectioned using a diamond saw to produce a thin transverse section. This was mounted on a glass microscope slide and then examined using low power microscopy to count the opaque zones. The count, the estimate of relative width of the most recent increment and the time of year of capture were interpreted together to provide the estimate of fish age (McGlennon et al. 2000).

Data processing

The sizes and ages of Snapper were used to generate regional, annual estimates of size and age structures. The regions considered were Northern Spencer Gulf (NSG), Southern Spencer Gulf (SSG), Northern Gulf St. Vincent (NGSV), Southern Gulf St. Vincent (SGSV), the south-eastern region (SE Region) and the west coast of Eyre Peninsula (WC) (Fig. 9.1). The analytical procedures that were used to develop these were the same as those used by McGlennon et al. (2000) and were based on computational procedures developed by Davis and Walsh (1995). The first objective for data analysis for each region and year was to develop an annual size structure, based on the fish measured from the commercial fishery but weighted according to the sizes of the catches taken by handline and longline, as the gear types were used to target different size classes of fish. An age/length key was generated for each region and year, based on the sizes and ages of fish that were sampled during that year from each region, regardless of season and gear type. The age/length key was then applied to the size frequency distribution to generate an annual, region-specific age structure. These annual age structures were compared graphically.

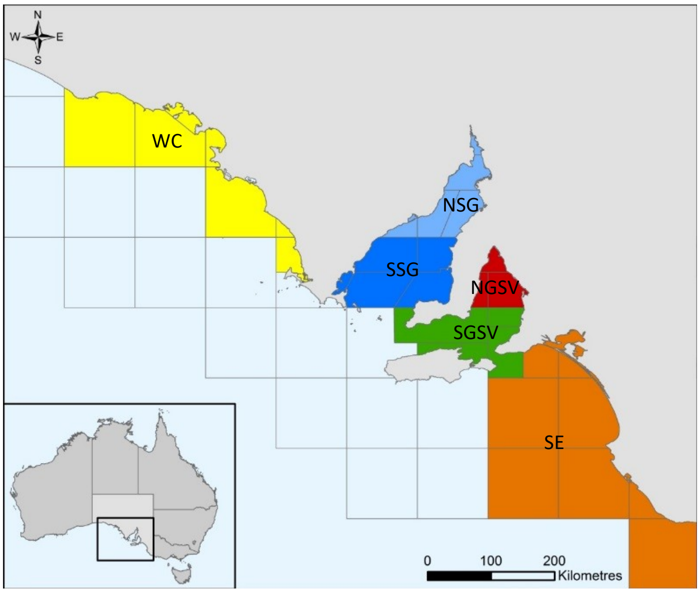

Fig. 9.1. Map of South Australia showing the division of the State's coastal waters into six regions; NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – south east Region, WC – west coast of Eyre Peninsula. The Marine Fishing Areas are shown as grey lines.

A significant component of the stock assessments for Snapper in South Australia involves updating and running the computer fishery model SnapEst (Fowler et al. 2020). This is a dynamic, spatial, age- and length-structured model that integrates several data sources to estimate time-series of output parameters (McGarvey and Feenstra 2004). The latter constitute important biological performance indicators that are assessed against reference points that are specified in the management plan as indicators of fishery status (PIRSA 2013). The regional, annual population size and age structures are important input data sources to the model. SnapEst integrates the numerous data sets and interprets them in terms of population processes, ultimately producing maximum likelihood estimates of the four biological performance indicators of: i). fishable biomass; ii). numbers of recruits; iii). harvest fraction; and iv). egg production. The estimates of numbers of recruits are the numbers that reach two years of age from particular year classes, thereby constituting relative estimates of year class strength.

The SnapEst model was recently updated and run for the stock assessments undertaken in 2020 and 2022 (Fowler et al. 2020, Drew et al. 2022). It incorporated the regional size and age structures that were generated up to and including 2020 and 2022, respectively. For both assessments, the model was run at the spatial scale of ‘stock’ (Chapter 10). As the stocks involve regional populations for which size and age data were collected, such data were integrated to provide outputs at the scale of stock. Estimates of recruitment time series were strongly dependent on the regional age structures and were highly informative about the population processes that have occurred at the scale of ‘stock’ over approximately the past 40-years.

For the five regions of NSG, SSG, NGSV, SGSV and the SE, the size-at-age data collected between 2000 and 2012 were used to generate region-specific von Bertalanffy growth curves. The “R” software package for statistical computing was used to fit the non-linear equation to the data and to generate estimates of L_∞, K and t_0. The growth curves for NSG and SSG were compared, as were those from NGSV and SGSV. This was done using the method of Kimura (1980), based on the 95% confidence regions of the von Bertalanffy growth parameters L_∞, and K.

9.3 Results

9.3.1 Ageing studies – 1970s and 1980s

In 1977, Dr Keith Jones was appointed as Program Leader of the Marine Scalefish Program of the Department of Fisheries of South Australia. From November in that year, he initiated a study into the growth and movement of Snapper in NSG. In that study, which continued throughout the 1980s, the ages of Snapper were determined from the structure of their scales. Fish scales were collected through a commercial market sampling program at the SAFCOL fish market, as well as during research cruises when Snapper were being tagged.

The collection of scales from Snapper and their processing and interpretation (Jones 1987), were developed from methods used at that time in New Zealand (Longhurst 1958, Paul 1976). For each fish, four to five scales were collected from near the pectoral fin. They were cleaned in NaOH solution and mounted between glass microscope slides. They were read with a microfiche reader from which information was transferred via overhead transparency film to an electronic digitizing pad. The distances between the scale nucleus and the rings were measured using the software package 'Autocad'. The relative scale radius to fish lengths were plotted and regression analyses were used to back-calculate estimates of length-at-age for each group of fish.

Between the late 1970s and mid-1980s, the numbers of Snapper that were aged from their scales gradually increased, from which the estimates of von Bertalanffy growth parameters and longevity were updated (Jones, 1981, 1984, 1987). By 1987, Snapper up to 31 years of age had been determined from their scales. The success rate of scale readings was 82%, although those with >15 annual rings were the most difficult to read because of the closeness of the outer rings as well as accretion of calcium in the centre of the scales that made it difficult for light to penetrate through them. Von Bertalanffy growth parameters were estimated using the 'FISHPARM' software package based on the mean lengths of age from back-calculated lengths-at-age. Low sample sizes were available for fish whose ages were estimated to be >26 years old. Jones (1987) estimated the von Bertalanffy growth parameters to be; L_∞ = 89.5 cm, k = 0.057, t_0 = -1.24.

Despite that fish scales were used for numerous years to age Snapper in different jurisdictions, concern began to emerge about the accuracy of the age estimates (Ferrell and Morison 1993). This culminated in comparisons being done between counts from scales and otoliths. These comparisons gave some ambiguous results. One comparison done in South Australia showed remarkable agreement in the counts between scales and sectioned otoliths for fish estimated to be up to 33 years of age, although sample sizes were low for fish older than 13 years (Ferrell and Morison 1993). Alternatively, a later comparison showed an age-dependent bias with counts of rings in scales under-estimating those from sectioned otoliths for older fish (McGlennon et al. 2000).

When the numbers of rings in the scales exceeded 19, they under-estimated those in otoliths by counts of between three and 18. Furthermore, considerably more scales from older fish were rejected as unreadable compared to the sectioned otoliths. Researchers in South Australia and New Zealand reported geographic differences in the clarity and interpretability of both types of structures (Ferrell and Morison 1993).

9.3.2 Ageing studies – 1990s and 2000s

Over the past 30 years, population studies for Snapper in South Australia that considered ages of adult fish have essentially used the same ageing methodology, i.e., for each fish a transverse section was cut from the centre of the sagitta and the structure of the newly exposed otolith surface was interpreted in terms of fish age in years (McGlennon et al. 2000, Fowler and McGlennon 2011, Fowler et al. 2020). The consistency in the basic ageing methodology over the 30+ year period related to the continuity in tenure of the senior technician (WBJ) throughout most of this period. Otherwise, some changes in the ageing studies did occur which related to an increase in geographic scale and to the QA/QC procedures that were applied, as described below.

Development of ageing protocol

To avoid the ‘process’ errors that were described above, an important contribution to developing a direct ageing protocol based on otoliths is the consideration of ‘validation’ that the results accurately reflect the true age of the fish. This involves addressing three criteria that the otoliths must fulfill before they can be reliably used in a fish ageing protocol (Fowler 1990): the otoliths must display an internal structure of increments; this structure must correspond to a regular and determinable time scale; and the otoliths must continue to grow throughout the lives of the individual fish, so that the incremental structure being interpreted relates to the duration of their lives. These three criteria are considered here with respect to the transverse sections (TS-sections) of otoliths for ageing Snapper from South Australian waters.

Criterion 1: otoliths must display an internal structure of increments

The TS-sections of sagittae of Snapper when illuminated with transmitted light display a complex macrostructure (Fig. 9.2). The centres of the sections that form during the early life history stages are dark, dense, and opaque (Chapter 8, Francis et al. 1992a). Outside of this, they generally have lower opacity throughout which there is an alternating sequence of opaque and translucent zones, the counts of which vary amongst otoliths. Also, there is considerable variation amongst otoliths from different fish with respect to the clarity and interpretability of these different zones. For those that are particularly clear, the alternation between opaque and translucent zones can be abrupt and distinct with little obvious gradient in opacity (Fig. 9.2).

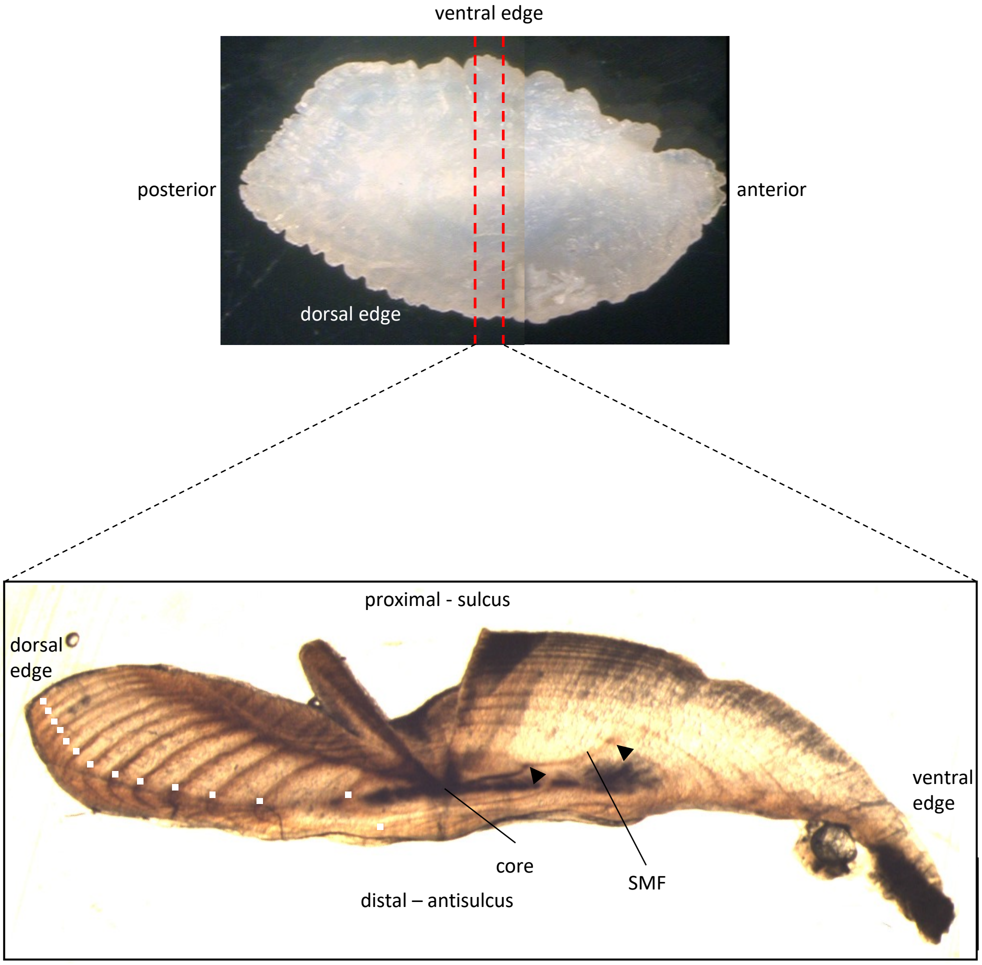

Fig. 9.2. Photomicrographs of Snapper otoliths. Top – Distal surface of a whole sagitta illuminated with reflected light. The area removed as the TS-section is indicated with dashed lines. Bottom – TS-section of sagitta illuminated with transmitted light, so the opaque zones are dark and translucent zones are light. The marked opaque zones towards the dorsal edge relate to fish age. SMF- refers to the pigmented curved strip relating to the sagitta-subcupular meshwork fibres. Dark arrows between the core and the ventral edge indicate inflection points that correspond to the first and second annual opaque zones.

Criterion 2: otolith structure must be related to a regular and determinable time scale

There are numerous techniques for determining the periodicity of increment formation in fish otoliths (Campana 2001). For South Australia, the most comprehensive study of the structure and growth of Snapper otoliths involved a combination of ‘edge analysis’ and ‘marginal increment analysis’ that was undertaken for two year-classes of fish from NSG (Fowler and Schilling 2004). For many otoliths from the strong 1991 and 1997-year classes that were sampled almost weekly between September 2000 and December 2002, the characteristics of the edges of the otoliths were compared monthly. Each otolith was considered along two axes, i.e., at the dorsal apex and on the dorsal side of the sulcus (Fig. 9.2). For each axis, the edge type was recorded (opaque or translucent) and the width of the marginal increment was measured relative to the penultimate increment. Across the two year-classes, this considered the formation of the 5th and 6th increments as well as the 11th and 12th increments. There were several results from these analyses:

- for most otoliths from both year classes sampled throughout the year, the edges were translucent. The numbers of otoliths with opaque edges peaked in late spring and early summer, with some variation in timing between age classes, i.e., for the 5th and 6th increments the edges were opaque around November/December, whilst for the 11th and 12th increments, they were opaque around October/November;
- marginal increment analysis indicated that the otoliths continued to grow throughout the year, but the growth rate was seasonal, with growth in width and thickness greatest during summer, declining through autumn and relatively low in winter and spring.

For the two year-classes of Snapper that were sampled over an 18-month period, the periodicity and timing of formation of the opaque zones in otoliths were considered. The conclusions were: that the opaque zones formed yearly during late spring and summer, with variation in timing related to age. The conclusions were consistent with findings from a study undertaken for Snapper from NSG sampled in 1991 and 1994 (McGlennon et al. 2000), which showed that the otoliths with opaque margins were recorded between November and February.

The two studies that undertook ‘edge’ analysis of otoliths (McGlennon et al. 2000, Fowler and Schilling 2004), were done for Snapper from NSG. Similar detailed studies have not been done for other South Australian regions. Despite some regional variation in the clarity and interpretability of the incremental structure of otoliths, nevertheless several validation studies for other places provide confidence in the generality of the conclusion about the periodicity of increment formation. Such validation studies were undertaken in New South Wales and New Zealand (Ferrell et al. 1992, Francis et al. 1992b). These based on treating fish with tetracycline, which leaves a fluorescent time-marker in the otoliths (Campana 2001, Wright et al. 2002). For the New South Wales study, growth of otoliths from young-of-the-year Snapper was greatest during spring and summer, whilst opaque zones were apparent in the otoliths during winter, becoming visible between June and October (Ferrell et al. 1992). For the New Zealand study, annual periodicity of increment formation was demonstrated for fish up to 30 years of age (Francis et al. 1992b). This conclusion was supported by the growth of tagged fish as well as year-to-year consistency in year class strength. Also, for Snapper from New Zealand, the macrostructure of alternating opaque and translucent zones in otoliths was related to the underlying microstructure of daily increments (Francis et al. 1992c). For Snapper of one to three years of age, the opaque zones related to periods during which the daily increments were too narrow to be resolved with light microscopy, i.e., during winter. This is consistent with the opaque zones forming seasonally once per year. For otoliths older than three years, daily increments were generally not resolvable in either the opaque or translucent zones. This is consistent with the decline in the widths of annual increments with age.

Criterion 3: otoliths must continue to grow throughout the lives of fish at a perceptible rate

The purpose of this criterion relates to the fact that as fish age their somatic growth slows down. If, simultaneously, the growth of the otoliths also slows to a point of being imperceptible throughout the remaining lifetime of the fish, then a count of the increments will no longer be indicative of total age. In several studies, one done in New Zealand (Francis et al. 1992d) and the other in South Australia (McGlennon 2003), the morphometrics of Snapper otoliths were considered. The relationships for both otolith length and width with age reached asymptotes, indicating that otolith growth in these planes did slow down to potentially imperceptible levels. Nevertheless, in both studies, there were linear relationships between otolith weight and estimated age. This reflected that despite the slowing of otolith growth in length and width, there were still relatively consistent thicknesses of new material added to the proximal surfaces of the otoliths on an annual basis. This results in the ‘stacking’ of annual increments that is apparent in the TS-sections of otoliths of older Snapper (Fig. 9.3). These two studies have demonstrated that it is necessary to consider the plane along which otoliths are interpreted to ensure accurate interpretation. By the early 1990s, ageing protocols for Snapper in most jurisdictions of Australia and New Zealand were based on TS-sections of otoliths, although at that time in Queensland a combination of whole otoliths and TS-sections were being used to age the different age classes of fish (Ferrell and Morison 1993).

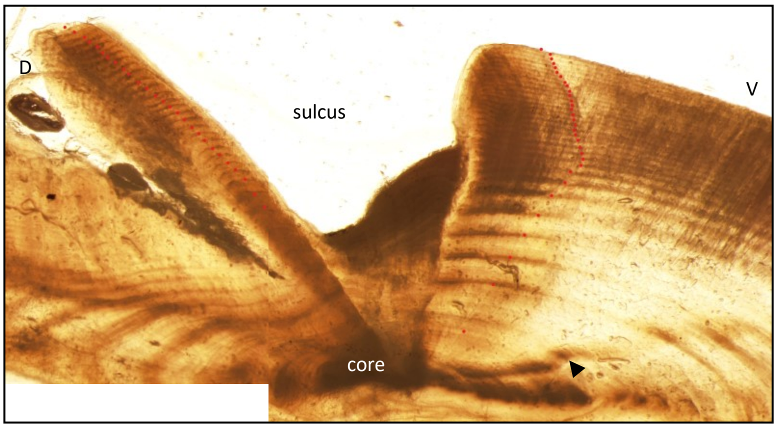

Fig. 9.3. Photomicrograph of TS-section from a Snapper otolith showing the annual increments ‘stacked’ towards the distal surface from the core. The opaque increments are marked (red dots) on both the dorsal and ventral sides of the sulcus. The dark arrow shows the inflection point in the SMF that relates to the formation of the first opaque zone.

Interpretation of otolith structure to determine fish age

To interpret the macrostructure of otoliths in terms of fish age, it is necessary to identify all of the annual increments, and to know their periodicity and timing of formation (McGlennon et al. 2000, Fowler 2009). The latter two of these points were considered for Snapper in the discussion on validation above. The first point is significant since the appearance of the annual increments can differ with age, particularly as the first one or several can be more diffuse in appearance than the latter 'stacked' increments that are discernible in TS-sections (Fig. 9.3) (Fowler 2009). Ironically, this means that when using the TS-sections of otoliths it may be easier to age older fish than younger ones, as the sequence of increments can be more easily distinguished. If the first increment is incorrectly identified this means that the point at which the count is started will be wrong, resulting in incorrect estimates of age (Campana 2001).

For Snapper otoliths, there is a method for identifying the first increment. In the TS-sections, there is a distinct, dark-brown, curved strip that runs from near the core to the ventral-sulcal margin (Figs. 9.2, 9.3). The contrast with adjacent sagittal material usually decreases with distance from the core. It was suggested that this pigmented curved strip developed from a point on the sagittal margin that has a relatively high-density fibre connection between the sagitta and the subcupular meshwork of the otolithic membrane, which may act as a pivot point for sagitta movement (Francis et al. 1992a). The pigmented curved strip was called a zone of sagitta-subcupular meshwork fibres (SMF), referring to its hypothesised origin. The significance of the SMF is that there is a notable inflection point that corresponds to the growth of the otolith during its first winter (Figs. 9.2, 9.3). This helps identify the first increment. Furthermore, in some sagittae, a second weak inflection point is visible at the second opaque zone (Fig. 9.2). Since the early 1990s in most jurisdictions of Australia and New Zealand, the SMF has been used to interpret the structure of the TS-sections (Ferrell and Morison 1993).

The assignment of age to an otolith depends on interpreting its edge and the width of the marginal increment, relative to the assigned birthday. For Snapper in South Australia, a birthday of 1st January is used, which falls approximately mid-way through the annual reproductive season (Chapters 2 and 3). From the results of 'edge' analysis of these otoliths, as described above, this is also around the time when the opaque zone forms. As such, the correct interpretation of an otolith, in terms of fish age, relies on knowing when the fish was captured, as well as whether the otolith edge is translucent or opaque and a relative estimate of the width of the marginal increment. This is most challenging for those fish that are captured through late spring and summer, the period during which the opaque zone forms. For such fish, it is necessary to decide whether: the otolith has a wide translucent zone reflecting that the new opaque zone has not yet formed; the opaque zone is forming and is currently on the otolith edge; or the opaque zone has recently formed and there is a narrow translucent zone on the edge. The otolith edge type and date-of-fish-capture ultimately determine the increment count that is used to calculate fish age. In New Zealand, an algorithm was developed to calculate fish age based on the increment count, the timing of the year and width of the marginal increment (Francis et al. 1992). This algorithm was also used in South Australia for assigning fish age during the 1990s (McGlennon et al. 2000).

Quality control, assessment, and precision of age estimates

As indicated above, interpreting the structure of otoliths in terms of fish age can be challenging, because of the complexity of their structure (Campana 2001, Morison et al. 2005). As such, even once an ageing protocol has been established through the assessment of otolith growth and appropriate validation procedures, ageing errors will still occur that reflect incorrect interpretation of the otolith structure. Since interpreting otolith structure is a skill that must be learned and developed, the rate of ageing errors is likely to differ amongst personnel.

For ageing studies on Snapper in South Australia, the focus on QA and QC procedures has varied over time. In the written reports from ageing studies based on fish scales that were done in the late 1970s and 1980s, there was little mention of issues around QA/QC apart from statements about the proportion of scales that were successfully interpreted (Jones 1981, 1984, 1987). For example, Jones (1987) indicated that for 250 sets of scales collected from both gulfs through commercial market sampling, a count was obtained for 82%. Those that were most difficult to interpret had counts of >15, with the difficulty in interpretation relating to the closeness of the outer rings and accretion of calcium in the centre, which limited the transmittance of light. In a later study, scale interpretability was related to ring count (McGlennon et al. 2000). Whilst ~20% of scales with one to five rings were assigned low readability indices, this increased to 52% for scales with >12 rings. In contrast, considerably fewer of the TS-sections of otoliths from the same fish were rejected.

In the 1990s, TS-sections of otoliths were counted using a binocular microscope with transmitted light (McGlennon et al. 2000). The QC procedures involved otoliths being interpreted by multiple readers, who considered the otoliths independently and without knowledge of fish size or capture date. For each otolith, the reader recorded: the count of annuli; the edge type (opaque or translucent); and a readability index of 0 – 4, relating to increasing clarity. The counts from the TS-sections from fish sampled in 1991 were first compared between two readers. A third reader then considered those otoliths for which the counts disagreed. A count was accepted when there was agreement between the 2nd and 3rd readers. However, when disagreement again occurred, the TS-section was considered jointly by both readers and either a final count was agreed upon or the otolith was discarded. Of the 512 otoliths considered in that year, counts were agreed for 382, i.e., 74.6%. The counts were compared between readers using age-bias plots (Campana 2001), which demonstrated no systematic bias between readers for fish up to 36 years of age. Furthermore, the counts from readers were generally very close, which resulted in small confidence intervals.

For fish from the 1994-year class, the TS-sections were also read by two readers (i.e., Readers 2 and 3 from above). When disagreements on counts or edge type occurred, the otoliths were re-

read jointly, and agreement reached, or the otolith was discarded. The comparisons between readers again indicated no systematic bias between readers and there was similarity in counts up to 33 years and small confidence intervals.

For both the 1991 and 1994-samples, the precision of independent counts were evaluated by calculating the coefficient of variation (CV) for the multiple counts for individual otoliths and averaging the CVs within each count group. The overall mean CVs for the 1991 and 1994 samples were 2.61% and 1.94%, respectively (McGlennon et al. 2000).

Reference Collection

Through the late 1990s and early 2000s, the concept of using reference collections of otoliths was developed as a significant component of QA-QC procedures for fish ageing studies (Campana 2001). A reference collection is a selection of otoliths of 'known' age or 'consensus-agreed' estimates of age. They have two main applications in fish ageing studies: for monitoring the consistency in age determinations by readers over the short-term and long-term; and for training purposes. The otoliths that comprise the reference collection should be representative of the numerous factors that can influence otolith clarity and interpretability and the relative widths of their increments, such as; age, sex, size, season and year, and region of collection. Systematic or biased errors are of considerable concern in ageing studies because of their consequences for calculating parameters that relate to population dynamics. Reference collections are used to test for short-term and long-term bias and precision in estimates of fish age. The age-bias plot provides an age-by-age measure of deviation between age readings that are being compared. Ageing precision is defined as the repeatability of age estimates. Measuring such precision is a valuable means of assessing the reproducibility of a reader's age determinations or of comparing the skill levels between readers. One of the most widely used measures of precision in ageing work is the average percent error (APE) (Beamish and Fournier 1981, Campana 2001, Fowler 2009).

In June 2008, a reference collection of TS-sections of Snapper otoliths was established at the South Australian Aquatic Sciences Centre (SAASC). Between 2000 and 2008, sagittae from approximately 10,000 Snapper were collected from South Australia's marine coastal waters in the regions of NSG, SSG, NGSV, SGSVS, SE and WC, primarily from commercial market sampling. For the development of the reference collection, the TS-sections of several hundred of these were selected randomly, to ensure that otoliths from the different regions, age classes and readability indices were represented approximately in proportion to their contribution to the overall collection. Some older otoliths were also selectively added, to ensure their representation. Since all otoliths had previously been considered in the systematic ageing work, an estimate of age already existed in the biological database. All selected otoliths were then re-read by one of two experienced readers (AJF, WBJ). When there were disagreements in age estimates, the otoliths were re-read together to resolve differences and to develop an 'agreed' age for each fish. A database relating to the reference collection was developed that included the estimate of ‘agreed’ age as well as other information. At this early stage, the reference collection involved 297 otoliths. In October 2010, the reference collection and database were updated with a further 197 otoliths that were collected between June 2008 and October 2010, bringing the total number of TS-sections to 494, all collected between 2000 and 2010.

Since 2008, at SAASC there have been several otolith readers responsible for the systematic ageing of Snapper. They adopted the following methodology in applying the reference collection. On each occasion of use of the reference collection, a number of otoliths were randomly selected for consideration. The TS-sections were examined and counted to provide the ‘trial’ estimates of age. The latter were then compared with the ‘agreed’ age estimates from the database, using statistical and graphical procedures. To achieve this on each occasion, an Excel spreadsheet (Apply reference collection.xls) was used to guide the user through the various steps. The first worksheet allowed the user to nominate the number of otoliths that would be considered and to generate random numbers to select the TS-sections to be considered. These TS-sections were then read to produce ‘trial’ estimates of age. Then, the second worksheet was populated by the reader with the ‘agreed’ and ‘trial’ estimates of age, the differences between which were used to calculate the APE. The final worksheet used the same results to generate the age-bias plot, to assess for any age-related bias.

Table 9.1. Results from the use of the Snapper otolith reference collection in South Australia for assessing age-related bias and precision in otolith interpretations. For each occasion, the table shows the number of TS-sections considered, the number of disagreements between the ‘agreed’ and ‘trial’ age estimates, the maximum difference between the two estimates of age, the estimates of average percent error, and whether there was age-related bias evident in the age-bias plot.

Reader	Date	No. TS-sections	Age range (years)	Number that disagree	Maximum difference	APE	Age-bias
1	Jun 2008	50	2 – 30	10	2	1.2	No
1	Oct 2008	49	2 – 35	11	2	2.9	No
1	Feb 2009	50	2 – 33	8	3	1.6	No
1	Jun 2009	50	2 – 30	6	1	1.3	No
1	Sep 2009	50	3 – 34	13	2	1.2	No
1	Oct 2014	50	2 – 31	13	3	4.1	No
2	Aug 2009	50	2 – 33	13	2	0.9	No
2	Sep 2009	50	2 – 35	15	4	1.4	No
2	Apr 2010	50	2 – 33	14	1	0.9	No
2	Nov 2010	50	2 – 30	7	1	0.61	No
2	Mar 2011	50	2 – 33	12	2	0.82	No
2	Jun 2011	50	2 – 35	10	3	1.29	No
2	Nov 2011	50	2 – 35	10	3	1.46	No
2	Aug 2012	50	2 – 35	8	2	0.59	No
2	Oct 2013	50	2 – 31	4	1	0.76	No
2	May 2014	50	2 – 34	9	2	1.59	No
2	Aug 2014	50	2 – 31	9	2	0.66	No
2	Nov 2014	50	2 – 31	8	7	1.18	No

In the application of the ageing protocol for Snapper, the reference collection has been used on numerous occasions to test for consistency in otolith interpretation. The intention was that the otolith readers would test themselves against the reference collection approximately every three months or when there had been a considerable break since they had last worked with Snapper otoliths. For each test, the otolith readers considered 50 otoliths. For this purpose, the Snapper reference collection was used by two readers most consistently between 2008 and 2014 (Table 9.1). Generally, on each occasion, 50 otoliths were examined, for which the age range was from 2 to >30 years. The percentages of disagreements between ‘agreed’ and ‘trial’ ages ranged from 8 to 30%. The extent of these differences was generally small, involving counts of only one or two. However, for one otolith, the difference was seven (Fig. 9.4). This exceptional difference is difficult to understand in the light of the other results, and now cannot be resolved as the person is no longer a staff member at SAASC. The estimates of APE ranged from 0.59% to 4.1% but were generally below 2%. These are low for a species with such an extensive age range of >30 age classes (Campana 2001). The age-bias plots consistently demonstrated no age-related bias that would indicate long-term drift in the interpretation of the otoliths (Fig. 9.4).

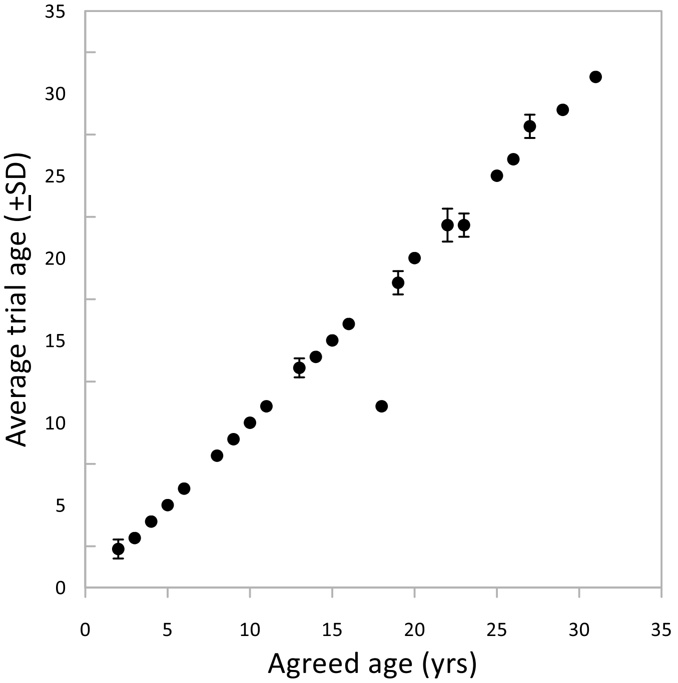

Fig. 9.4. Age-bias plot from comparison between ‘trial’ ages and ‘agreed’ ages of a sample of TS-sections of otoliths from the reference collection, undertaken in November 2014 by Reader 2. The otolith for which there was a difference in counts of seven is evident. There is no indication of age-related bias.

9.3.3 Regional, annual population age structures

Since 2000, the adult sampling for Snapper in South Australia has resulted in many thousands of fish having been measured, of which a significant subset has been aged from their otoliths. From these, annual size and age structures have been developed for numerous years for each of NSG, SSG, NGSV, SGSV and the SE Region (Appendix Figs. A9.1 – A9.5) and most recently for the WC (Appendix Fig. A9.6). The annual size structures reflect modes of fish in four size categories, i.e., ‘small’ fish in the 30 – 40 cm CFL range, ‘medium’ fish that were 40 – 60 cm CFL, ‘large’ fish that were 60 – 80 cm CFL and ‘very large’ fish that were >80 cm CFL. The age structures indicate that the populations consisted of multiple age classes, with consistency in relative year class strength amongst years. These size and age structures provide important insights into the demographic processes that sustain the regional populations. The following text summarises the variation in size and age structures amongst years for the different regions.

Northern Spencer Gulf

For NSG, the sample sizes for the Snapper that were measured and aged declined considerably over the years, reflecting the reduction in regional abundances and the fewer fish that were passing through the SAFCOL fish market. There were considerable changes to the size structures over the years (Fig. A9.1). Between 2000 and 2015, the populations were dominated by the 'small', 'medium' and 'large' size classes, although with some variation in modal structure over time. From 2016 to 2019, the size structures primarily involved 'small' fish, less so the 'medium' fish, with only very minor representation of the 'large' and 'very large' size classes. In 2021, the size distribution was uniform across the 'small', 'medium' and 'large' size categories.

Characteristically, in each year, the age structures involved multiple age classes that ranged from 2 to 33 years in age, of which a few were more numerous than most others. This reflected variation in year class strength and the persistence of several strong year classes that contributed to catches over numerous years. From 2000 to 2010, the strong year classes had recruited in 1991, 1997 and 1999, the latter two of which continued to dominate until 2015 (Fig. A9.1). By 2017, these two strong year classes were depleted, and the age structures mainly involved fish that had recruited between 2012 and 2016. Between 2018 and 2021, it was evident that the 2014-year class was relatively strong, whilst in the latter two age structures, the 2017-year class emerged as another relatively strong year class.

Southern Spencer Gulf

Size structures for SSG are available for most years from 2000 to 2021. Whilst the sample sizes for fish measured have been variable, from 2010 onwards they have generally been low, reflecting the decline in regional catches. The annual size structures usually involved modes of 'small' and 'large' fish, whose relative sizes varied amongst years (Fig. A9.2). There were generally fewer 'medium' fish, whilst 'very large' fish were always rare in this region.

The age structures for SSG were generally dominated by one or several year classes with intervening year classes poorly represented (Fig. A9.2). From 2000 to 2005/06, the strong year classes had recruited in 1991 and 1997. From 2003, the 1999-year class began to emerge as another strong one. Between 2007 and 2014, the 1997 and 1999-year classes dominated the age structures. By 2015, these two year-classes had become depleted, and the age distribution involved fish across a range of year classes, particularly the 2006 year class. The age structure in 2020 was broad and involved strong year classes that had recruited in 2006, 2007, 2009 and 2014. The 2021 age structure further confirmed the strength of the 2014-year class and exposed the emergence of the 2017-year class as another relatively strong one.

Northern Gulf St. Vincent

Prior to 2007, the numbers of fish from NGSV that were accessed in the SAFCOL market were very low, which prevented consideration of size and age structures. Subsequently, the sample sizes were higher due to the increase in commercial catches (Fowler et al. 2020). This was the case until 2016, after which the sample sizes once again declined considerably (Fig. A9.3). For this region in each year, all four size classes were generally well represented in the size structures, although with some variation amongst years in their relative contributions (Fig. A9.3). In 2007 and 2008, the 'small' fish were most numerous, whilst in 2009 and 2010, the 'large' fish were most numerous. In 2011 and 2012, no modes were evident in the size structures, indicating that all size categories contributed to the catches. Then, from 2016 to 2022, the annual size structures were dominated by 'large' fish, with relatively few 'small', 'medium' and 'very large' fish compared to previous years. There is some suggestion of a contraction in size structure.

Population age structures were developed for most years from 2008 to 2022 (Fig. A9.3). These were generally characterised by a broad number of age classes. Furthermore, numerous strong year classes contributed to the catches in some years, which were consistent across a number of consecutive years. These were the 1991, 1997, 1999, 2001, 2004, 2006, 2007 and 2009-year classes. The age structures in 2017 showed the emergence of the 2014-year class, whose significance remained evident until 2022. Furthermore, the age structures in 2020, 2021 and 2022 indicated the likely significance of the 2017-year class as another strong one.

Southern Gulf St. Vincent

The sample sizes for Snapper from SGSV were variable, being relatively high until 2015 and then declining considerably. Between 2000 and 2020, the size structures varied considerably (Fig. A9.4). From 2000 to 2003, they were dominated by 'large' fish. Then, from 2007 to 2015, the strong modes were for the 'small' and 'medium' categories. From 2016 to 2019, modal structure was less evident in the size distributions, but suggest higher numbers of 'large' fish. In contrast, in 2020, 2021 and 2022, the size distributions were broad, but were dominated by the 'medium' fish.

Over the years, the age structures for SGSV were dominated by particular year classes. From 2000 to 2003, this was the 1991-year class, augmented with the emergence of the 1997-year class (Fig. A9.4). From 2007 to 2011, the strong year classes had recruited in 2001 and 2004, which were later augmented by the 2006 and 2007-year classes. By 2014, the 2009-year class had also emerged as a significant one. The age structures for 2017 and 2018 were dominated by fish that recruited between 2005 and 2010 but also showed the emergence of the 2014-year class. This was reinforced by the age structures for 2019 and 2020 that were dominated by the 2007, 2009 and 2014-year classes. The age structures for 2021 and 2022 were dominated by the 2014-year class, and also showed the emergence of the 2017-year class as another possible strong one.

South East

For the SE Region, size distributions are available for most years from 2008 to 2022 (Fig. A9.5). The sample sizes were relatively high prior to 2015, very low in 2017 and 2019, before they increased considerably in 2020 and 2021. The latter related to a SARDI observer program that operated on the commercial fishing vessels. The size structures to 2012 were dominated by 'small' and 'medium' fish, and rarely involved fish >60 cm CFL. For several years until 2017, there was a proportional increase in representation of 'large' fish. The size distributions for 2020 and 2021 involved large modes of 'small' and some 'medium' fish.

The age structures up to 2014 were dominated by the 2001 and 2004- year classes, whose relative contributions changed between 2009 and 2014 (Fig. A9.5). In 2015, the age structure was dominated by the 2007 and 2009-year classes. Those for 2019 and 2020 were both dominated by two pairs of year classes that had recruited in 2009 and 2010 and in 2013 and 2014, respectively. The age structures for 2021 and 2022 were dominated by the 2013 and 2014-year classes.

West Coast

For the WC, targeted sampling of Snapper was done in 2019, 2020 and 2021. There was an increasing number of fish sampled across these years for the development of size and age structures. Throughout these years, the size distributions were dominated by 'large' fish with very few sampled that were in the other size categories (Fig. A9.6). The fish covered a broad age range, including one captured in 2020 that was 27-years old. The age structures for each of the three years were dominated by several strong year classes. In 2019, these were the 2006, 2008, 2012 and 2014-year classes. Those in 2020, were the 2009, 2012 and 2014 year-classes, whilst in 2021, the 2014-year class was the clear dominate age class.

9.3.4 Annual recruitment rates

The annual estimates of recruitment numbers that were output by the SnapEst model were described in Chapter 7 and the stock assessment in 2020 (Fowler et al. 2020). The model output covered the time-period of 1983 to 2017. For the Spencer Gulf/ West Coast Stock (SG/WCS), the estimates were highly variable. There were periods of consecutive years when low recruitment occurred, i.e., throughout the 1980s, the mid-1990s, and throughout the 2000s. In contrast, there were several years that produced exceptional year classes, i.e., 1991, 1997 and 1999, when the estimated recruitment was many times higher than those of intervening years (Fig. 9.5a).

For the Gulf St. Vincent Stock (GSVS), there were numerous strong year classes between 1991 and 2009. Like the SG/WCS, these included the 1991, 1997 and 1999-year classes (Fig. 9.5b). However, there were also several strong year classes that recruited through the 2000s, including the 2001, 2004, 2006, 2007 and 2009-year classes. So, for this stock, there were eight strong year classes that recruited throughout a 19-year period during the 1990s and 2000s.

For the SE Region, the recruitment rates were typically very low but punctuated by several exceptional year classes. The two strongest were in 2001 and 2004, whilst the 2014-year class was also relatively strong (Fig. 9.5c).

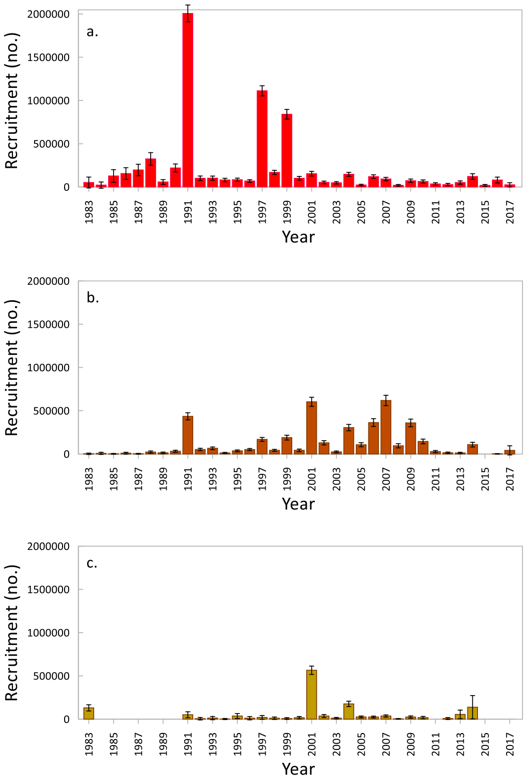

Fig. 9.5. Estimates of time-series of annual recruitment rates (+CI) from the SnapEst model in 2020 (Fowler et al. 2020). a. the SG/WCS. b. the GSVS. c. for the SE Region.

9.3.5 Regional analysis of growth

Analysis of growth was done at the regional spatial scale. The estimates of size-at-age and the resulting von Bertalanffy growth curves differed considerably amongst the five regions (Fig. 9.6). The two northern gulfs involved more older and larger Snapper than did the southern regions. For the latter regions, there were few fish encountered that were >15 years of age. Furthermore, for the southern gulfs, the estimates of size-at-age were generally distributed across a broader size range, indicating the presence of many more fish that were relatively small for their ages, i.e., slower growing, than was the case for the northern gulfs. The southern regions generally had lower estimates of L_∞, but higher values of K than the northern gulfs, but also involved higher estimates of standard error around the parameter estimates (Table 9.2). The exception was for SGSV for which there was a high estimate of L_∞, probably due to the dominance in the estimates of size-at-age of the younger age classes and under-representation of older fish, which prevented L_∞ from being well estimated. The resulting growth functions were compared between NSG and SSG and determined to be significantly different. This was also the case between NGSV and SGSV.

Table 9.2. Estimates of von Bertalanffy growth parameters for the five regions based on estimates of size-at-age for fish sampled between 2000 and 2012. Estimates of standard error are shown in brackets.

Region	L_∞	K	t_0
NSG	97.5 (0.95)	0.11 (0.003)	-0.699 (0.079)
SSG	67.3 (1.37)	0.17 (0.01)	-0.435 (0.264)
NGSV	92.6 (0.63)	0.14 (0.003)	-0.074 (0.065)
SGSV	104.5 (3.10)	0.08 (0.005)	-0.996 (0.157)
SE	88.0 (5.91)	0.065 (0.01)	-2.735 (0.630)

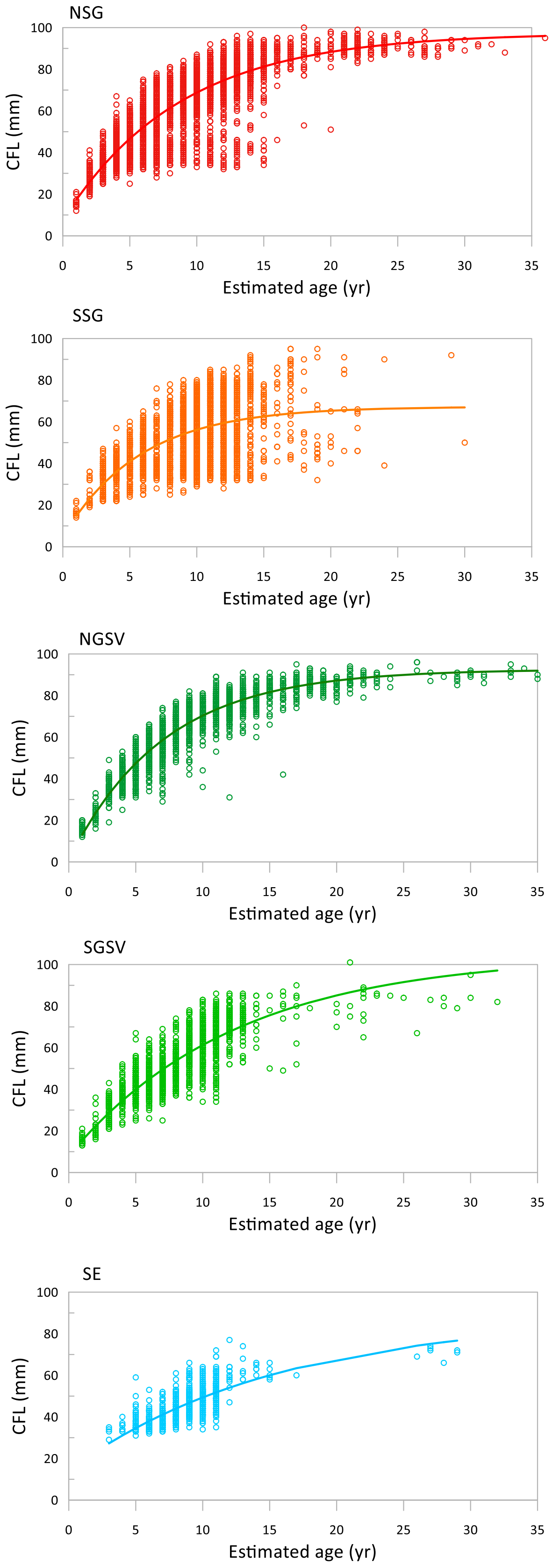

Fig. 9.6. Estimates of size-at-age and von Bertalanffy growth curves for the five regions for which age data were collected between 2000 and 2012.

9.4 Discussion

9.4.1 Validation considerations

The history of ageing studies for Snapper in South Australia constitutes part of the considerable history of research into the population biology of the species taken in the Marine Scalefish fishery. Soon after the commencement of Dr Keith Jones in 1977 in his position as program leader for the Marine Scalefish Fishery with the Department of Fisheries, he initiated market and research sampling to determine the size and age structures of Snapper in Spencer Gulf and later in Gulf St. Vincent. At that time and at least up until the mid-1980s, age determination was based on interpreting the rings in fish scales (Jones 1987). This reflected the ageing methodology that was being used for Snapper in New Zealand (Longhurst 1958, Paul 1976).

By the early 1990s, concerns had emerged about the accuracy of ageing Snapper using scales, because of the possibility of under-estimating the ages of older fish (Ferrell and Morison 1993). In South Australia, the ageing of Snapper was changed to being based on the alternating opaque and translucent zones in the TS-sections of the sagittae, the largest pair of otoliths (McGlennon et al. 2000, McGlennon 2003). The early work considered Snapper from NSG that were accessed by market sampling at the SAFCOL fish market in Adelaide. All subsequent ageing work has used the same technique (Fowler and McGlennon 2011, Fowler et al. 2020). During the 2000s, the spatial scale of sampling was expanded to include SSG, NGSV, SGSV, the SE Region and lately the WC. Since 2000, the sampling of Snapper populations from across the State's waters has resulted in: estimates of age for >20,000 Snapper; a repository of approximately 20,000 sectioned and whole otoliths; a database that includes ages for these fish as well as length measurements of nearly 75,000 fish; a reference collection and associated database of approximately 500 TS-sections.

There can now be considerable confidence in the age estimates from the TS-sections of the Snapper otoliths. Validation studies that used 'edge' and 'marginal increment' analyses of the otoliths (McGlennon et al. 2000, Fowler and Schilling 2004), showed they conformed to the three criteria that otoliths must fulfill to be useful in a fish ageing protocol (Fowler 1990). They display an alternating sequence of opaque/translucent zones that can be interpreted visually. There is an annual periodicity to the formation of each sequence of an opaque and translucent zone. Also, analyses of otolith growth determined that they continue to grow throughout a fish's life. Across years, otolith growth in weight is relatively consistent, which for older fish results in a consistent thickness of new material being added to the growing surface of the otolith annually, resulting in the 'stacked' appearance.

Based on the characteristics described above, the otoliths of Snapper from South Australia fulfilled the criteria to be used in a large-scale, systematic ageing protocol. The findings in this regard conformed to those from validation studies that were done in New Zealand and New South Wales

(Ferrell et al. 1992, Francis et al. 1992). For New Zealand, based on tetracycline tagging of fish across a broad age range, as well as a study of otolith morphometrics, the results were particularly convincing regarding the annual periodicity of increment formation and otolith growth throughout the fish's lives (Francis et al. 1992). Nevertheless, the timing of formation of the opaque zones varied amongst jurisdictions. In South Australia, the opaque zones formed primarily during the months of October to December (Fowler and Schilling 2004). For both northern and southern New Zealand, the timing was marginally earlier, i.e., between September and November, whilst for Sydney (New South Wales) it was earlier again, i.e., between June and October (Ferrell and Morison 1993). These geographic differences in timing were consistent with differences in the timing of reproduction (Chapter 3). This suggests a possible physiological influence on otolith increment formation rather than it being strictly an environmentally induced phenomenon.

There was one further feature in the structure of Snapper otoliths that provided a significant aid in their interpretation, whose significance relates to the potentially difficult task of identifying the first increment in the otolith structure (Campana 2001). The TS-sections of Snapper otoliths display a band of pigment called the zone of sagitta-subcupular meshwork fibres. Along this zone, there is an inflection point whose formation corresponds to the first opaque zone (Francis et al. 1992). This feature helps to avoid miscounting the increments, which could otherwise result in systematic errors in estimates of age due to the use of an incorrect starting point for the count.

9.4.2 QA/QC considerations

Whilst the combination of characteristics and features of Snapper otoliths that were described above means that the validation procedures were satisfactorily completed, nevertheless it is inevitable that some ageing errors will still occur (Morison et al. 2005). This is because of the inherent complexity in otolith structure and the variation in their clarity and interpretability. To ensure that such errors do not become systematic, i.e., are repeated consistently during the ageing process, appropriate QA/QC procedures must be implemented. For the ageing work done during the 1990s, such procedures involved using multiple readers who read the same otoliths, after which there was a process of reconciling counts that differed between readers (McGlennon et al. 2001). This approach to QA/QC is relatively expensive as it involves a multi-stage process that requires multiple handling and repeated reading of the same otoliths, as well as coordination between readers. Through the 1990s and 2000s, the concept of reference collections of otoliths was developed in other fish ageing labs around the world, as a means of overcoming such issues (Campana 2001).

In 2008, a reference collection was established for Snapper in South Australia using TS-sections of otoliths, which was later updated in 2010. It involves otoliths that were collected between 2000 and 2010 from the different regions of the State's waters. The otoliths were selected from across these broad temporal and spatial scales, so that typical otoliths with respect to their clarity and interpretability were included. In developing this collection, ‘agreed’ consensus ages were established between two experienced otolith readers. The reference collection has subsequently been used to train new readers of Snapper otoliths. However, it was primarily used in the first place as a QA measure by otolith readers to ensure that their interpretation of otolith structure remained consistent over time, i.e., did not show age-related, long-term drift. Between 2008 and 2014, the otolith readers used the reference collection on a near-quarterly basis for this purpose. In general, the resulting age-bias plots showed no evidence of such drift, whilst the estimates of APE showed that the age estimates demonstrated an acceptable level of precision.

9.4.3 Age-based population characteristics

Age-based population data were considered here either at the scale of stock or at the regional population level. Size and age structures were presented for the different regional populations for parts of the 21-year period from 2000 to 2020. The frequency distributions for each region showed considerable variation over time, reflecting the influences of demographic processes and events. Furthermore, this temporal variation was not consistent amongst regions, indicating that the demographic processes could differ at this larger, geographic spatial scale.

Between 2000 and 2012, NSG supported broad size and age structures that were consistently dominated by three strong year classes, i.e., those that recruited as 0+ fish in 1991, 1997 and 1999. From 2016 onwards, the population became truncated, as the size and age structures contracted towards the ‘small’ size category and relatively young fish that were associated with a few young age classes. No 0+ year classes that recruited throughout the 2000s, had the sustained impact on population structure across numerous years as did the three strong year classes of the 1990s.

For SSG, the extensive size range of Snapper that was evident in NSG throughout most of the 2000s was generally not evident, primarily relating to the lack of ‘very large’ fish in this region. This regional population was generally dominated by one or two strong year classes. From 2000 to 2014, these were the 1997 and 1999-year classes, i.e., the same ones that had dominated in NSG during the same period. After 2014, there were limited annual age structures available because the number of Snapper from this region that were accessed at the SAFCOL market was very limited. For this region, there was high variation in the estimates of size-at-age, which resulted in poor relationships between size and age.

From 2007, NGSV demonstrated very broad size structures from ‘small’ to ‘very large’ fish. This was the case until 2019 and 2020 when the fishery catches showed some indication of truncation. The age structures for NGSV showed numerous strong and consistent year classes, i.e., the 1991, 1997, 1999, 2001, 2004, 2006, 2007 and 2009-year classes, with some indication that the 2014 and 2017-year classes might be relatively strong. The population also had high estimates of longevity and a tight relationship between size and age.

Of the five regions, SGSV demonstrated the greatest variation in size structures, being dominated at various times by ‘small’, ‘medium’ or ‘large’ fish. These differences reflected the variation in ages of the dominant year classes over time. The SE Region also showed some considerable variation in size structures, but the population predominantly involved ‘small’ and ‘medium’-sized fish. From 2009, the population was dominated by the 2001 and 2004-year classes, and subsequently by several other year classes. From 2019 to 2021, the samples taken on the WC primarily involved ‘large’ fish that represented a broad range of age classes in each year. They showed evidence of the influence of several strong year classes.

It is evident from the descriptions above that for most regions, the population size and age structures demonstrated considerable variation over time. This variation reflected the influences of inter-annual variation in year class strength. Such variability is well documented for South Australian Snapper populations, relating to inter-annual variation in recruitment of the 0+ year class (Chapters 6, 7; McGlennon et al. 2000, Fowler and Jennings 2003). It is now well accepted that for Snapper, inter-annual variation in recruitment is one of the primary drivers for the population dynamics and fishery productivity at the regional scale. When the patterns of temporal variation in population size and age structures were compared over time there were some inter-regional similarities but also some differences. The 1991 and 1997-year classes were strong ones in each of NSG, SSG, NGSV and SGSV, whilst the 1999-year class was also strong in all but the latter region. The 2001 and 2004-year classes were particularly significant for the SE Region and were also important for NGSV and the SGSV, but far less so for NSG and SSG. In every region, the 2014-year class was a strong one, even for both the SE and the WC.

The size-at-age data presented in the regional growth curves indicated that the rates of growth and estimates of longevity for Snapper varied considerably amongst regions. The differences amongst regional estimates of longevity reflected that, in general, there were more old and larger Snapper found in the northern gulfs than the southern regions. These differences relate, at least partly, to regional differences in the growth patterns. ‘Dwarf’ fish, i.e., those that were small for their ages were a feature of the southern regions particularly SSG but were very rare in the northern gulfs. It is assumed that such fish are residents of the southern regions, and their slower growth reflects the different diets and physical environmental influences. This raises the issue about the movement of larger fish between the northern and southern gulfs. Whilst Snapper can move over distances of several hundred kilometres (Jones, 1981, 1984, McGlennon 2003), the significance of such movement on regional levels of biomass and population characteristics has only recent become evident (Chapter 10).

9.5 References

Beamish, R.J., Fournier, D.A. (1981). A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences 38: 982-983.

Brothers, E.B. (1982). Ageing reef fishes. NOAA national marine Fisheries Service Technical Memorandum. US Department of Commerce. NMFS-SEFC-80:3-23.

Campana, S.E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59: 197-242.

Campana, S.E., Thorrold, S.R. (2001). Otoliths, increments and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries and Aquatic Sciences 58: 30-38.

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

Eklund, J., Parmanne, R., Aneer, G. (2000). Between-reader variation in herring otolith ages and effects on estimated population parameters. Fisheries Research 46: 147-154.

Ferrell, D., Morison, A.K. (1993). Proceedings of a workshop on ageing snapper (Sparidae: *Pagrus auratus*). Marine Science Laboratories, Victorian Fisheries Research Institute. 39 pp.

Ferrell, D.J., Henry, G.W., Bell, J.D., Quartararo, N. (1992), Validation of annual marks in the otoliths of young snapper, *Pagrus auratus* (Sparidae). In ‘Age Determination and Growth in Fish and Other Aquatic Animals’. (Ed. D.C. Smith). Australian Journal of Marine and Freshwater Research 43: 1051-1055.

Fowler, A.J. (1990). Validation of annual growth increments in the otoliths of a small, tropical coral reef fish. Marine Ecology Progress Series 64: 25-38.

Fowler, A.J. (2009). Age in years from otoliths of adult tropical fish. In: Tropical fish otoliths: information for assessment, management and ecology. (Green, B.S., Mapstone, B.D., Carlos, G., Begg, G.A. eds.). Springer.

Fowler, A.J., McGlennon, D. (2011). Variation in productivity of a key snapper, *Chrysophrys auratus*, fishery related to recruitment and fleet dynamics. Fisheries Management and Ecology 18: 41-423.

Fowler, A.J., Schilling, K. (2004). Seasonal growth of otoliths from Snapper in South Australia. In: Fowler, A.J., Gillanders, B.M., Hall, K.C. Adult migration, population replenishment and geographic structure for Snapper in SA. Final Report to FRDC (Project No. 2002/001). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication Number RD 04/0163. 152 pp.

Fowler, A.J., Smart, J., McGarvey, R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111 pp.

Francis, M.P., Williams, M.W., Pryce, A.C., Pollard, S., Scott, S.G. (1992a). Daily increments in otoliths of juvenile snapper, *Pagrus auratus* (Sparidae). In ‘Age Determination and Growth in Fish and Other Aquatic Animals’. (Ed. D.C. Smith). Australian Journal of Marine and Freshwater Research 43: 1015-1032.

Francis, R.I.C.C., Paul, L.J., Mulligan, K.P. (1992b). Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection. In ‘Age Determination and Growth in Fish and Other Aquatic Animals’. (Ed. D.C. Smith). Australian Journal of Marine and Freshwater Research 43: 1069-1089.

Francis, R.I.C.C. Otolith radius is a poor predictor of age in adult snapper (*Pagrus auratus*). In ‘Age Determination and Growth in Fish and Other Aquatic Animals’. (Ed. D.C. Smith). Australian Journal of Marine and Freshwater Research 43: 1199-1202.

Jones, G.K. (1981). Biological research on snapper (*Chrysophrys auratus* syn. Unicolor) and an analysis of the fishery in northern Spencer Gulf. SAFIC 5 (6): 5 – 8.

Jones, G.K. (1984). A review of the commercial fishery for snapper (*Chrysophrys auratus*) in South Australian waters. A Discussion Paper. Department of Fisheries, South Australia. 29 pp.

Jones, G.K. (1987). Growth and size related movements of snapper (*Chrysophrys auratus*) in South Australian waters. (in prep.).

Jones, G.K. (1987). A review of the commercial fishery for snapper (*Chrysophrys auratus*) in South Australian waters (1983-1986). Discussion Paper No. 2. Department of Fisheries, South Australia. 20 pp.

Kimura, D.K. (1980). Likelihood methods for the von Bertalanffy growth curve. Fishery Bulletin 77: 765-776.

Lai, H.L., Gunderson, D.R. (1987). Effects of ageing errors on estimates of growth, mortality and yield per recruit for walleye Pollock (*Theragra chalcogramma*). Fisheries Research 5: 287-302.

Longhurst, A.R. (1958). Racial differences in size and growth in the New Zealand snapper. New Zealand Journal of Science 1(4): 487-499.

McFarlane, G.A., Beamish, R.J. (1995). Validation of the otolith cross-section method of age determination for sablefish (*Anoplopoma fimbria*). In: Secor, D.H., Dean, J.M., Campana, S.E. (eds). Recent developments in fish otolith research. University of South Carolina Press. Columbia, pp 319-329.

McGarvey, R., Feenstra, J.E. (2004). Stock assessment models with graphical user interfaces for key South Australian marine finfish stocks. Final Report to FRDC (Project No. 1999/145). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 176 pp.

McGlennon, D., Jones, G.K., Baker, J., Jackson, W.B., 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: 669-677.

McGlennon, D. (2003). The fisheries biology and population dynamics of Snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. PhD Thesis, University of Adelaide, Adelaide, South Australia. 212pp.

Morison, A.K., Burnett, J., McCurdy, W.J., Moksness, E. (2005). Quality issues in the use of otoliths for fish and age estimation. Marine and Freshwater Research 56: 773-782.

Wright, P.J., Panfili, J, Folkvord, H., Mosegaard, H., Meunier, F.J. (2002). Direct validation. In: Manual of fish sclerochronology. (Panfili, J., Pontual H (de), Troadec, H., Wright, P.J., eds), pp. 119-127. Brest, France: Ifremer-IRD coedition.

Paul, L.J. (1976). A study on age, growth, and population structure of the snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Bulletin No. 13. 62 pp.

PIRSA (2013). Management Plan for the South Australian Commercial Marine Scalefish Fishery. PIRSA Fisheries and Aquaculture, Adelaide, 143pp. The South Australian Fishery Management Series, Paper No. 59.

Power, G. (1978). Fish population structure in Arctic lakes. Journal of the Fishery Research Bord of Canada 35: 53-59.

9.6 Appendices

9.6.1 Annual regional size and age structures

The following series of figures show the annual size and age structures that were developed for the five regions of NSG, SSG, NGSV, SGSV and the SE, as well as a few for the WC. The data were collected primarily through market sampling but were augmented with samples of Snapper collected on scientific field trips. Samples considered from 2020, 2021 and 2022 that were captured from regions that were closed to fishing were captured in a targeted sampling program that involved commercial fishers, which was co-ordinated by SARDI.

Where size and/or age structures are not presented for a particular year, there were insufficient data collected during that year for their development. The age structures are presented by year class rather than age, which informs about the relative strengths of the different year classes, providing insight into the temporal variation in recruitment to the populations throughout the 20-year period. For each region and year, the sample sizes indicate the number of Snapper that were measured. Fewer fish were aged from their otoliths, and annual age/length keys were developed that were applied to the size structures to generate the age structures.

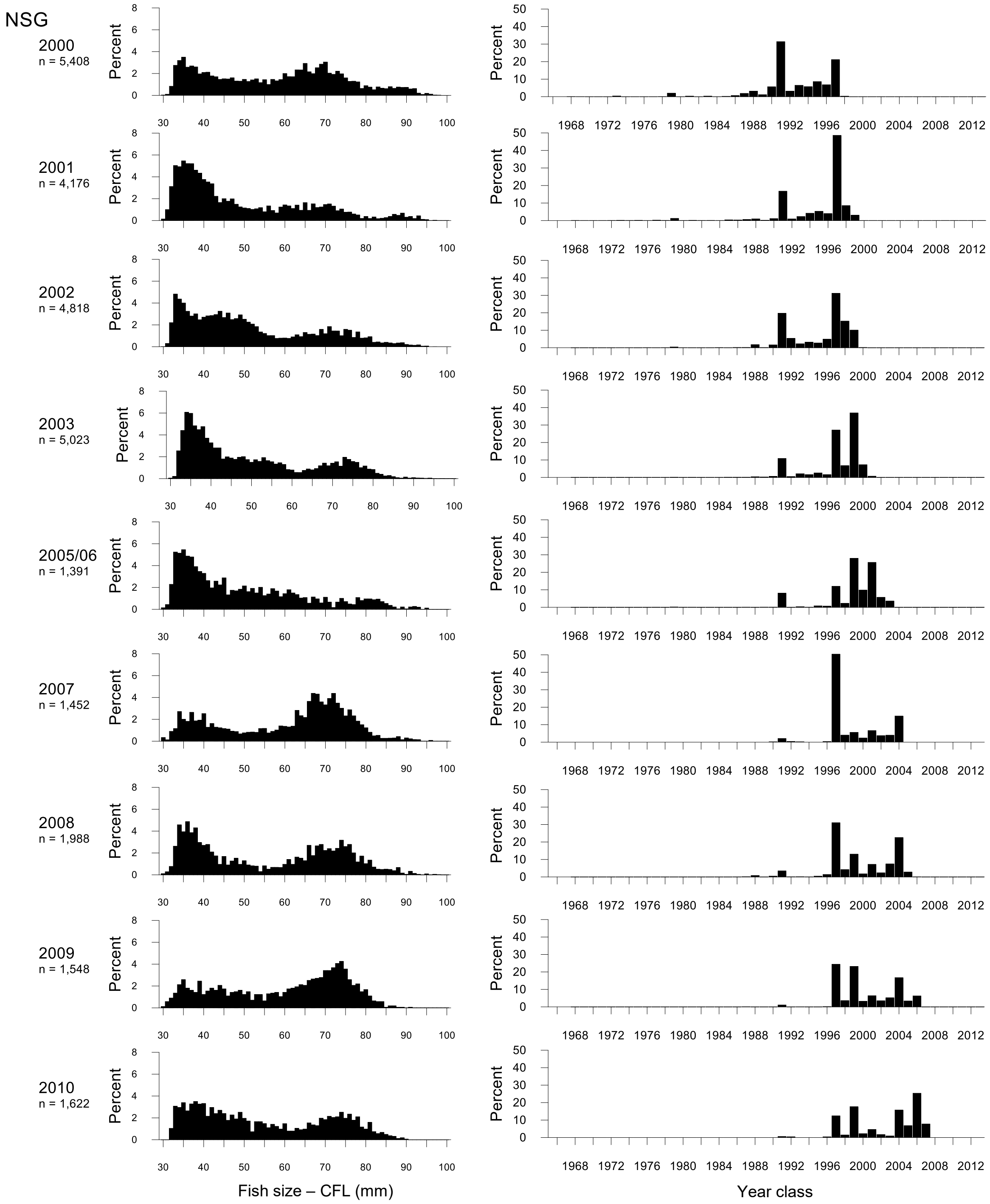

Fig. A9.1. Annual size and age structures for Snapper caught in NSG between 2000 and 2021. Left hand graphs show the size structures and the numbers of fish measured. Right hand graphs are the age structures showing the relative percentages of total catch accounted for by each year class, i.e., the years in which they recruited as 0+ fish.

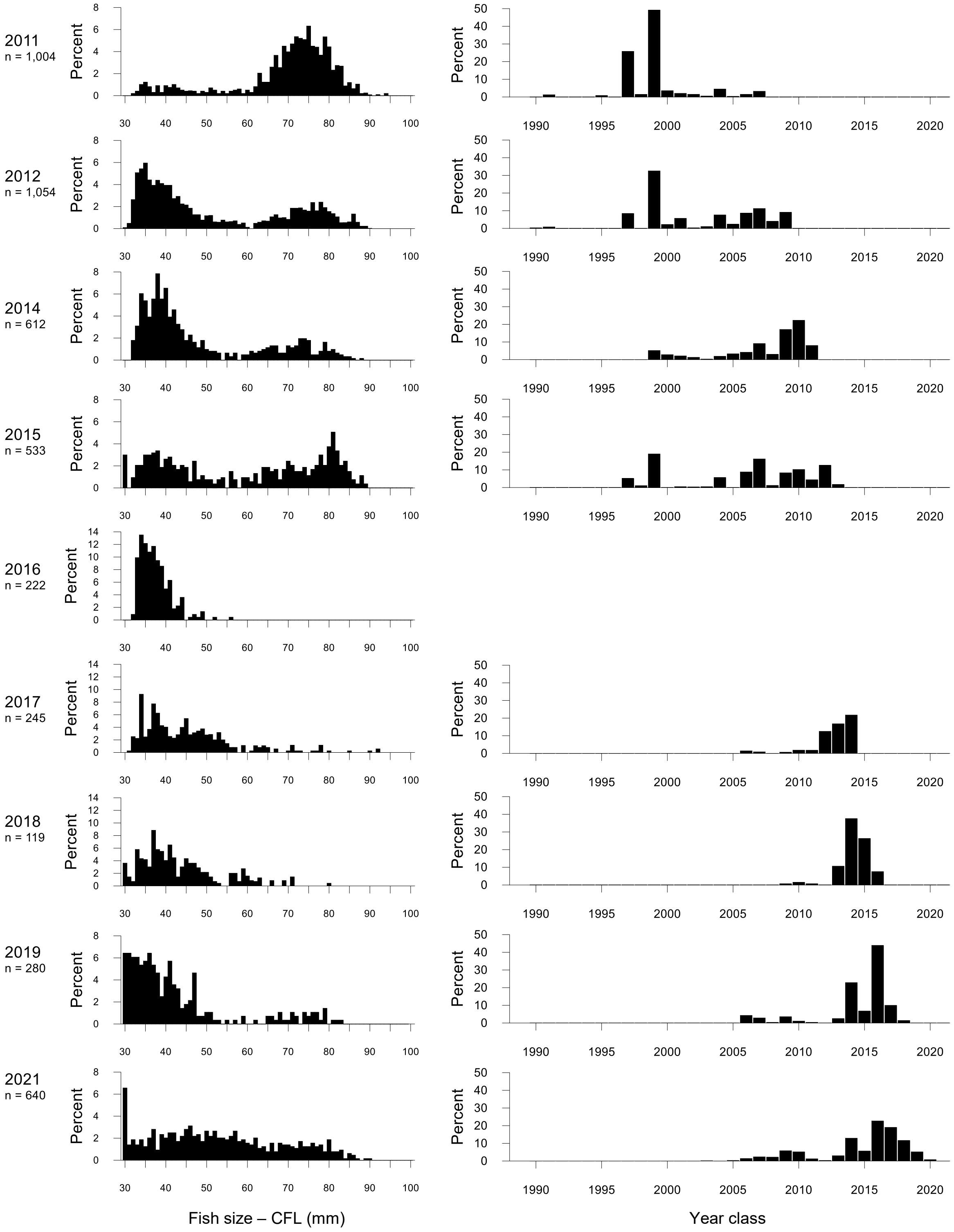

Fig. A9.1. continued for years 2011 to 2021 for NSG.

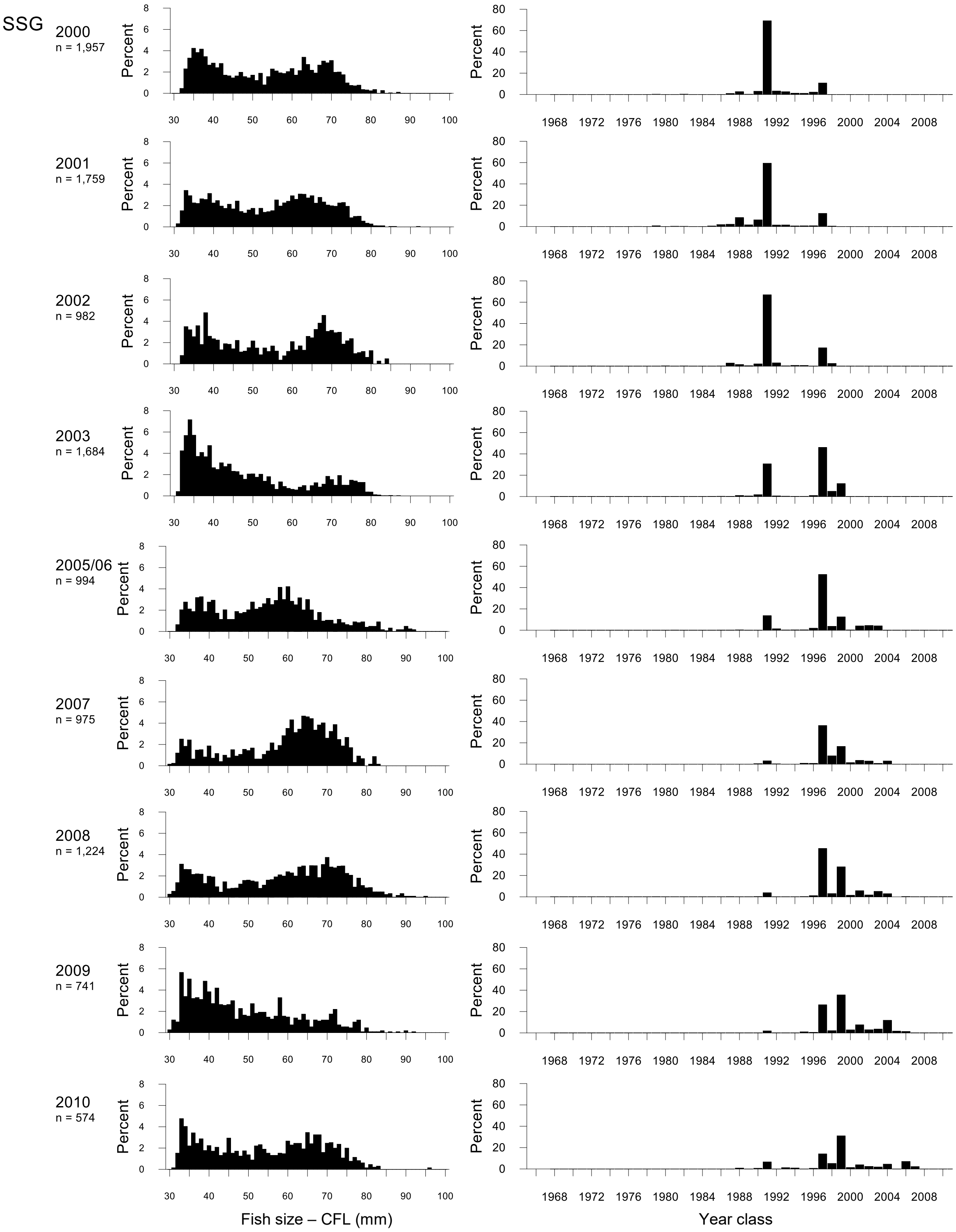

Fig. A9.2. Annual size and age structures for Snapper caught in SSG between 2000 and 2021. Left hand graphs show the size structures and the numbers of fish measured. Right hand graphs are the age structures showing the relative percentages of total catch accounted for by each year class, i.e., the years in which they recruited as 0+ fish.

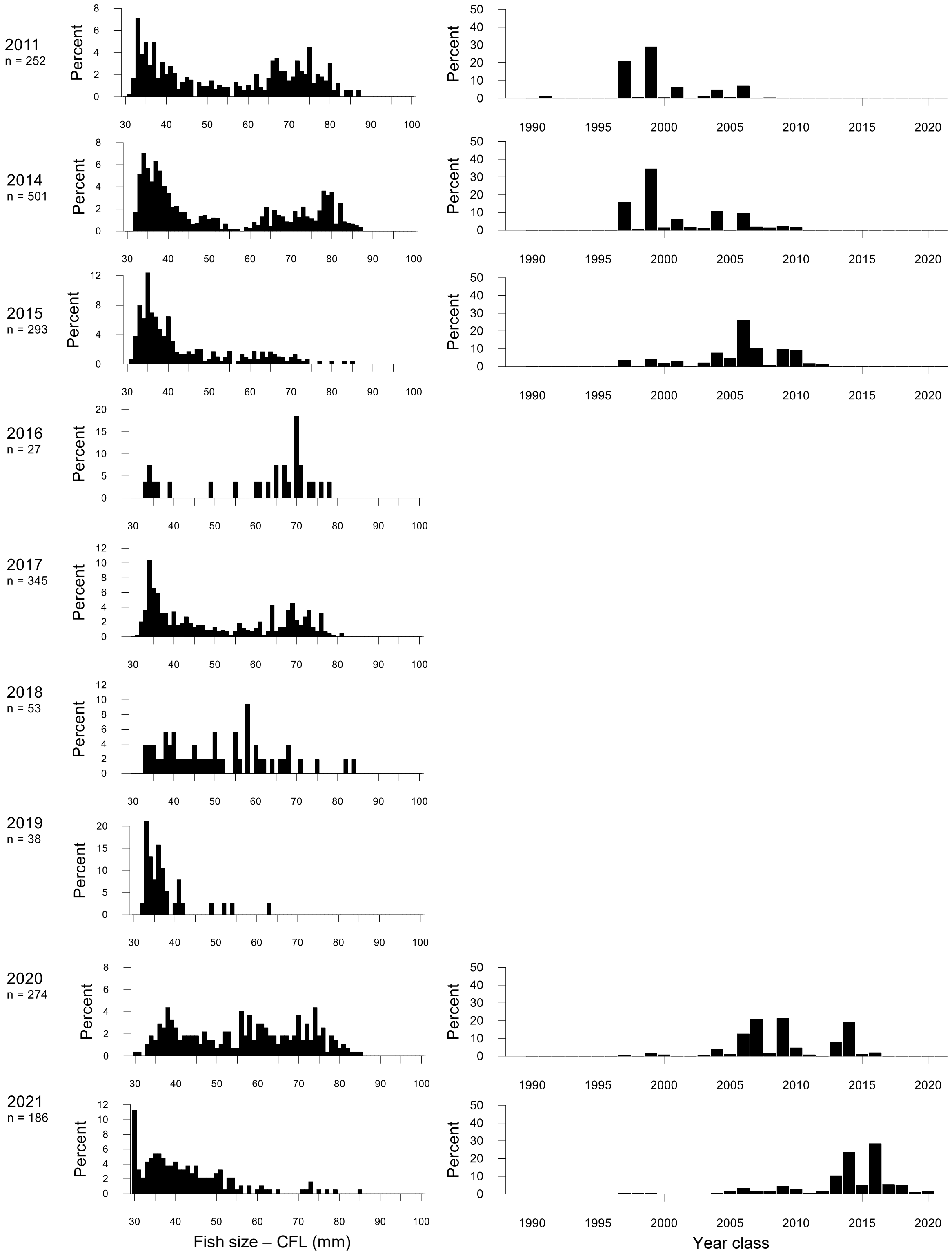

Fig. A9.2. continued for years 2011 to 2021 for SSG.

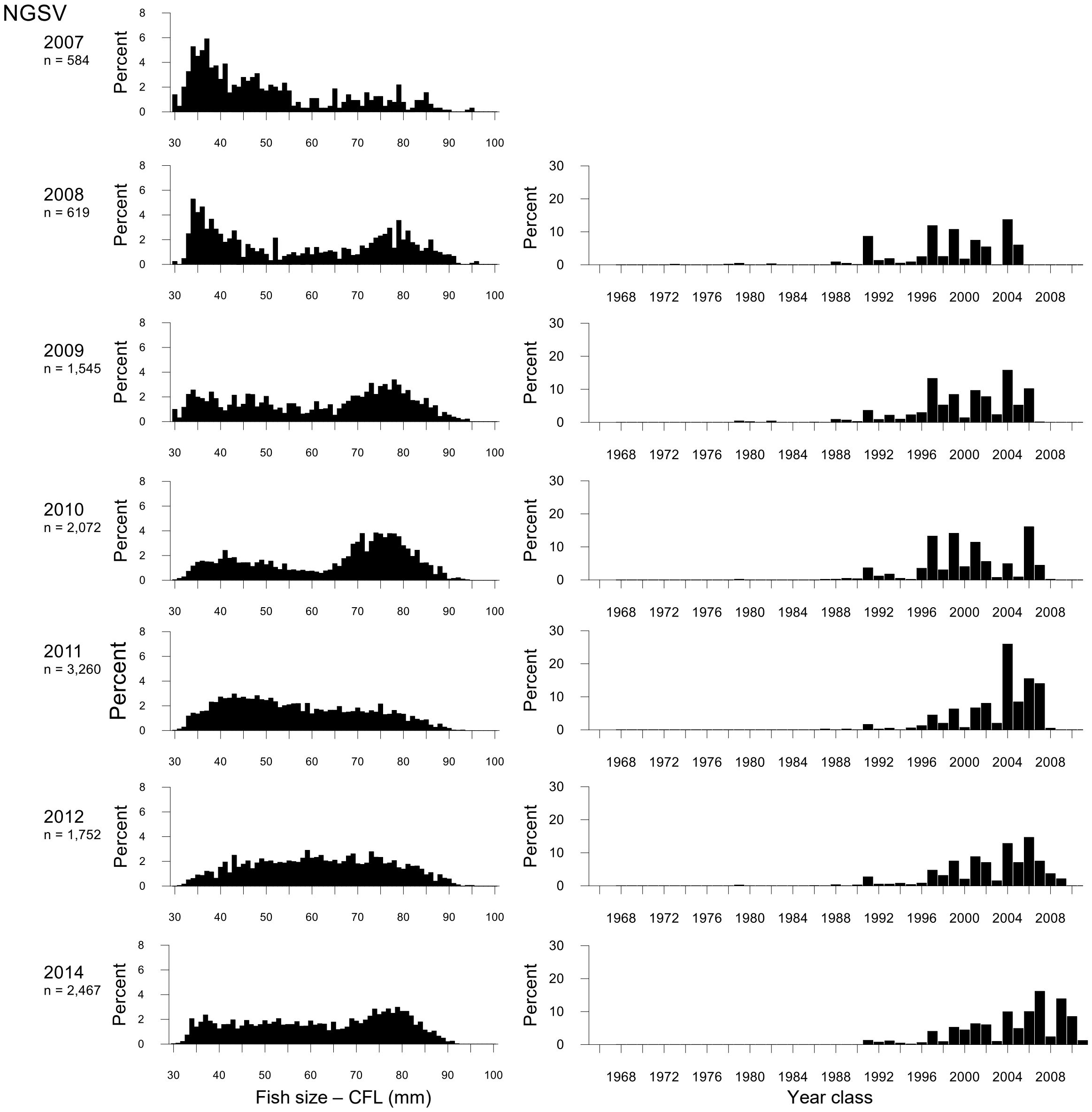

Fig. A9.3. Annual size and age structures for Snapper caught in NGSV between 2007 and 2022. Left hand graphs show the size structures and the numbers of fish measured. Right hand graphs are the age structures showing the relative percentages of total catch accounted for by each year class, i.e., the years in which they recruited as 0+ fish.

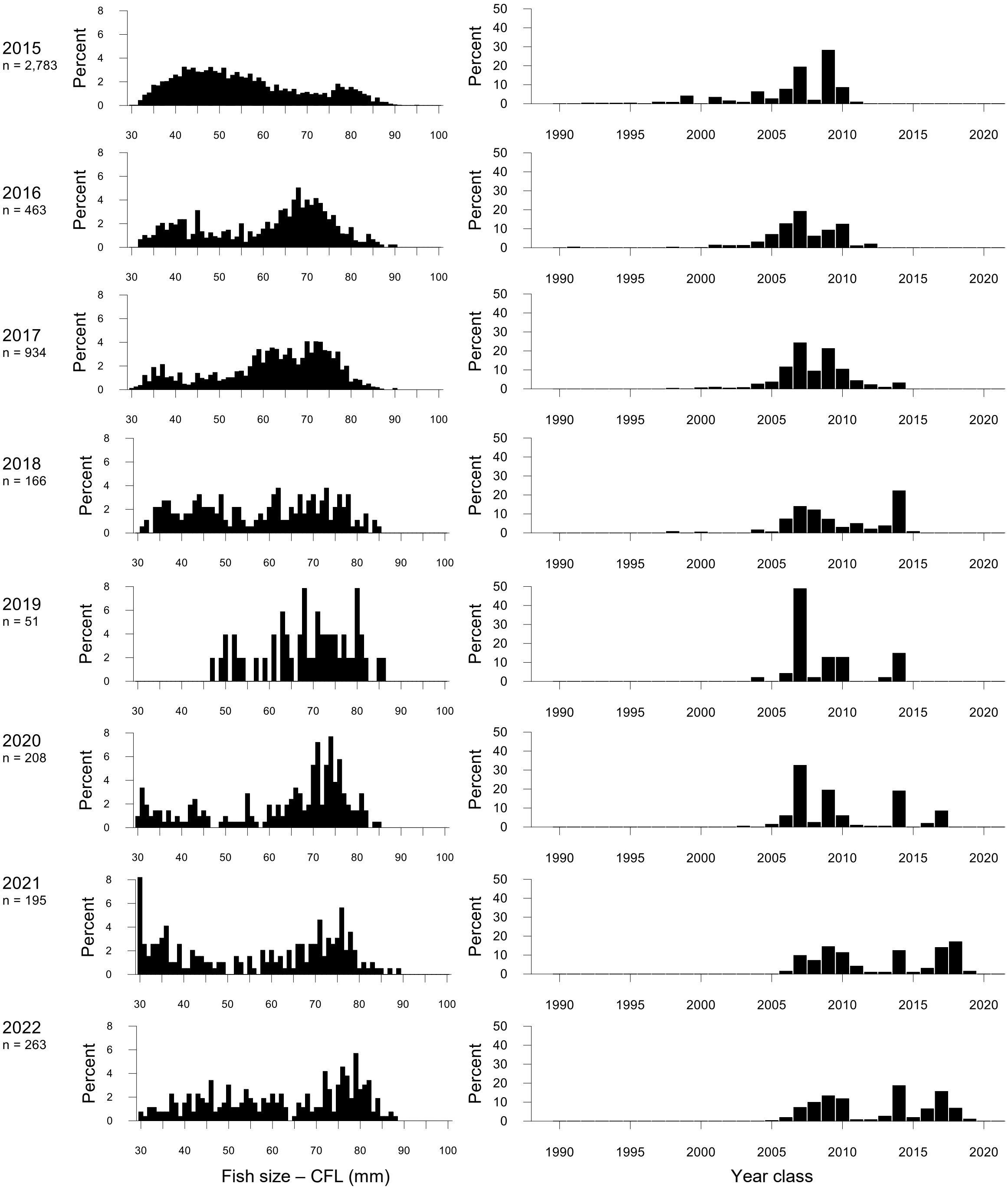

Fig. A9.3. continued for years 2015 to 2022 for NGSV.

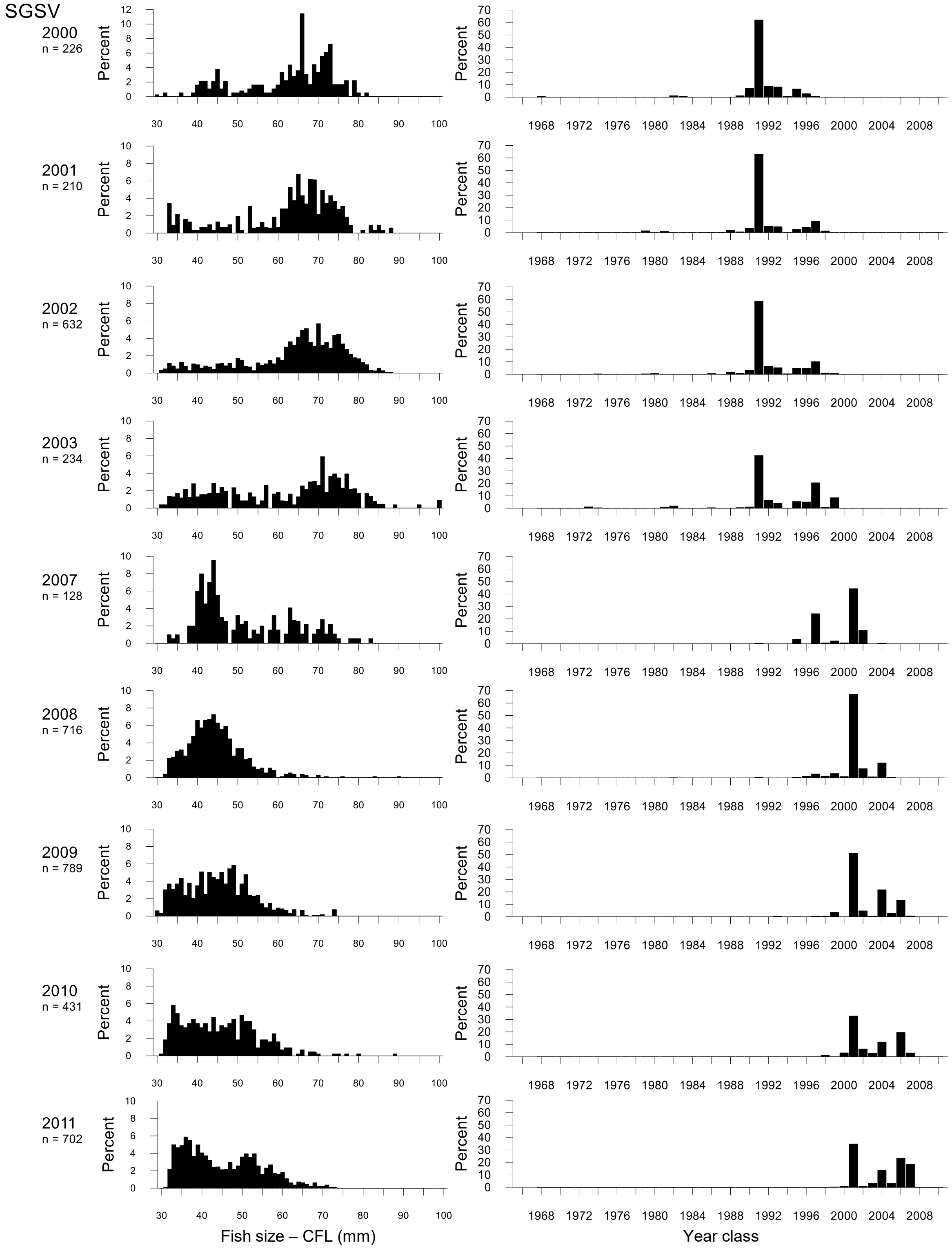

Fig. A9.4. Annual size and age structures for Snapper caught in SGSV between 2000 and 2022. Left hand graphs show the size structures and the numbers of fish measured. Right hand graphs are the age structures showing the relative percentages of total catch accounted for by each year class, i.e., the years in which they recruited as 0+ fish.

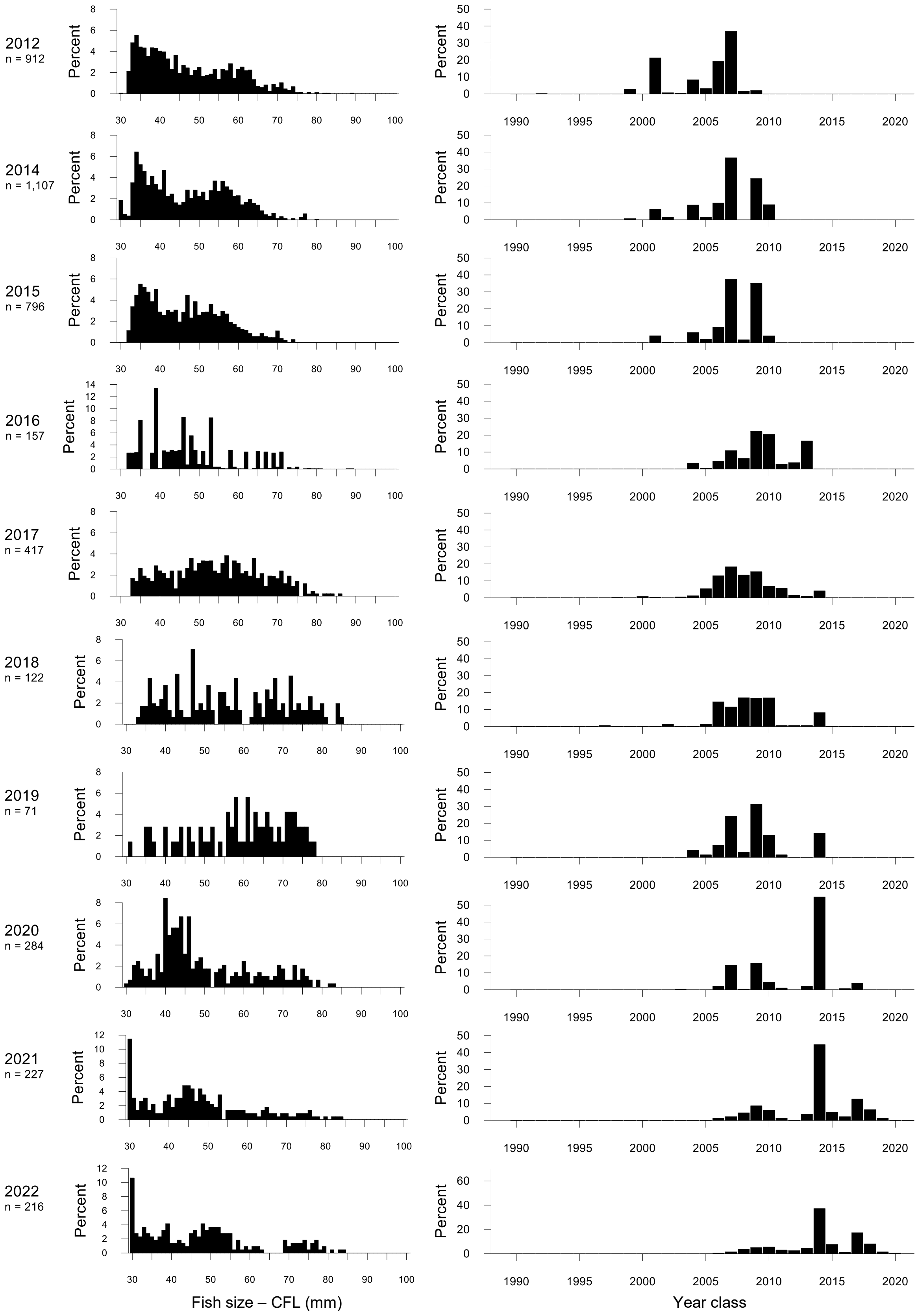

Fig. A9.4. continued for years 2014 to 2022 for SGSV.

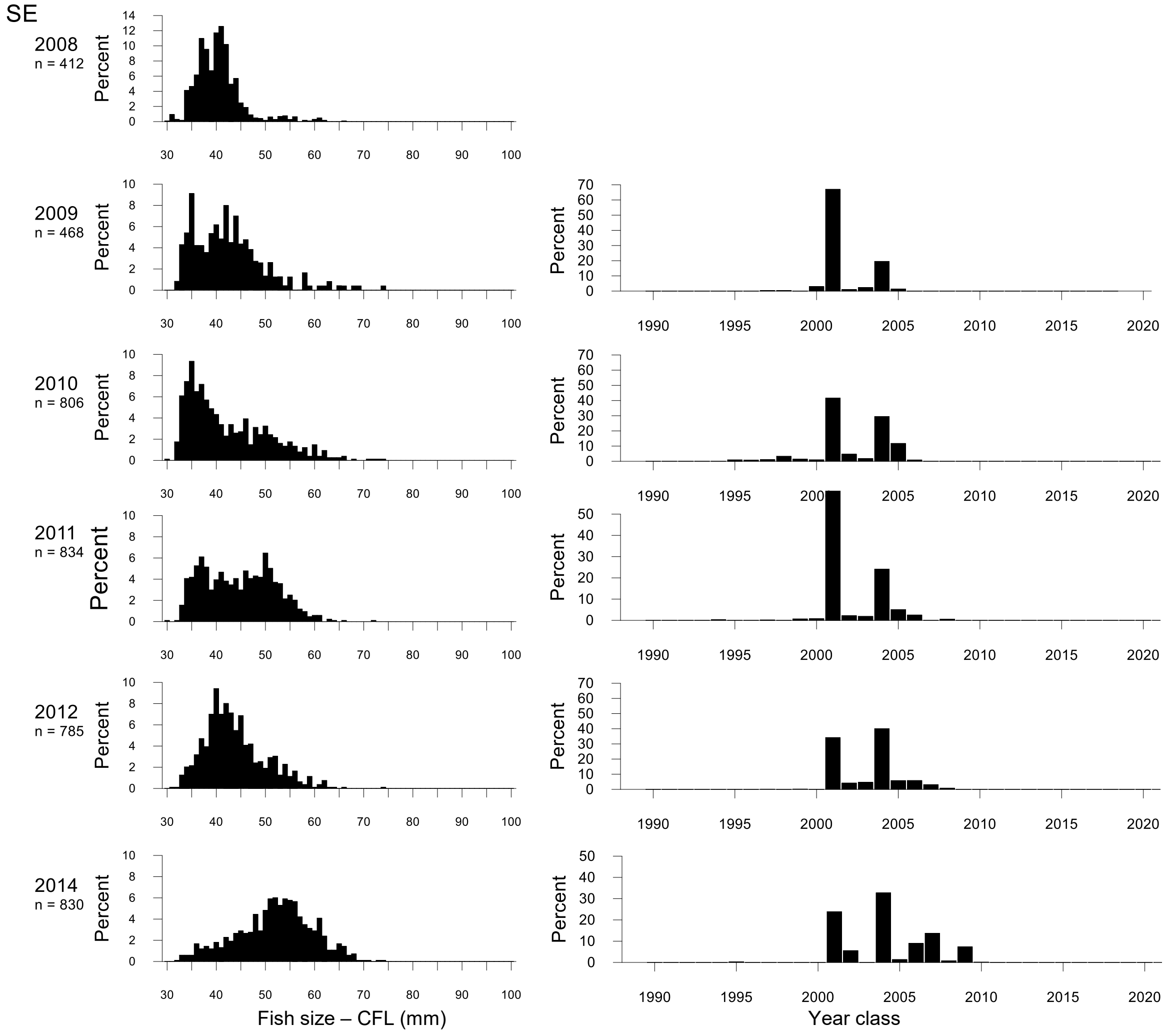

Fig. A9.5. Annual size and age structures for Snapper caught in SE between 2008 and 2022. Left hand graphs show the size structures and the numbers of fish measured. Right hand graphs are the age structures.

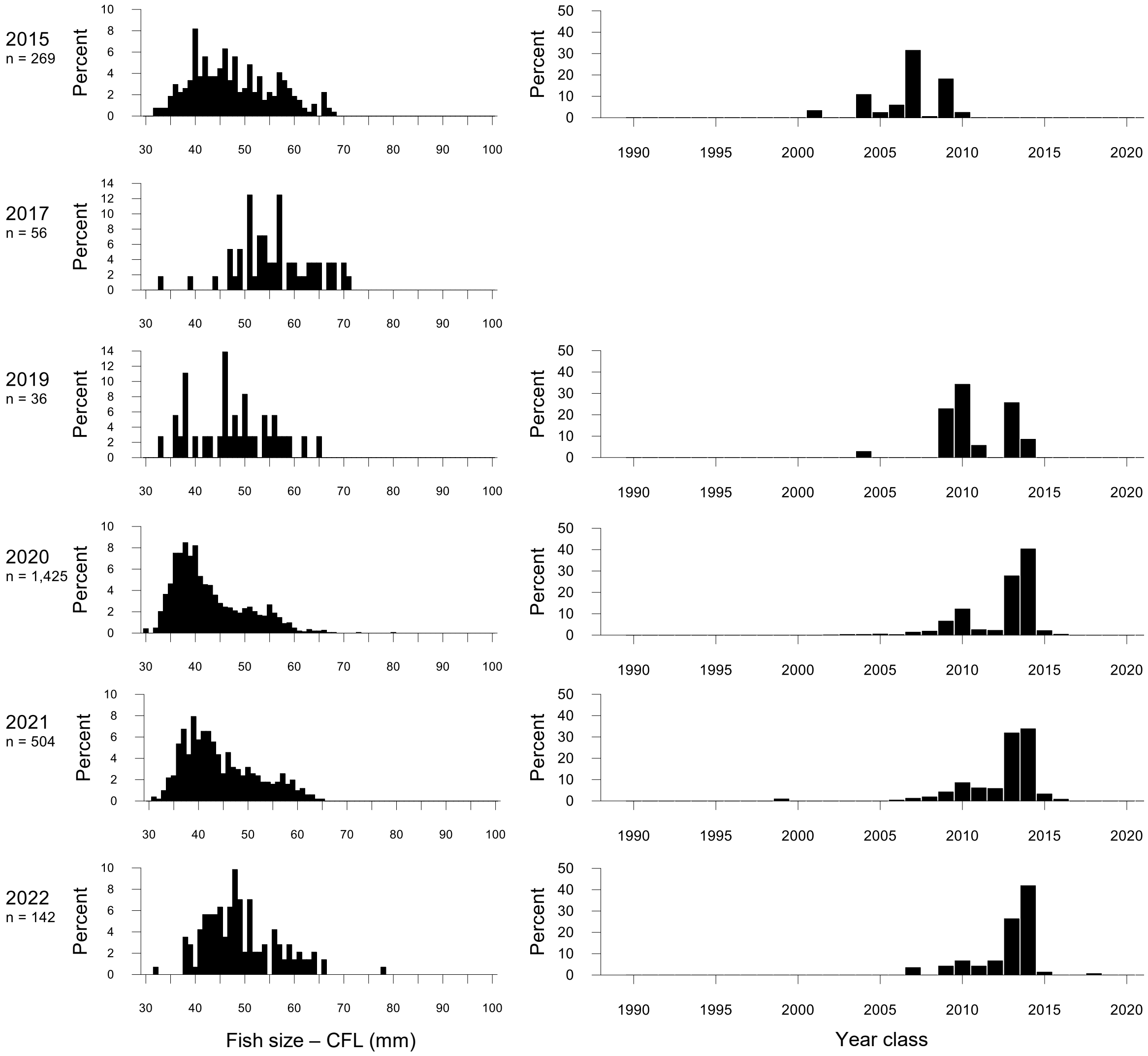

Fig. A9.5. continued for years 2014 to 2022 for SE.

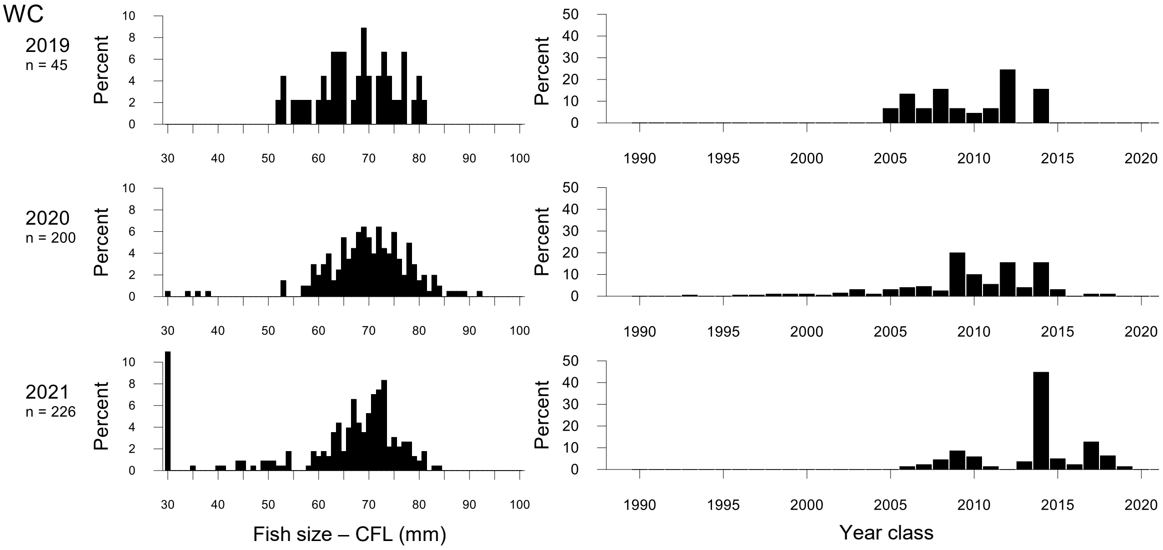

Fig. A9.6. Annual size and age structures for Snapper caught in WC between 2008 and 2021. Left hand graphs show the size structures and the numbers of fish measured. Right hand graphs are the age structures.

10. POPULATION CONNECTIVITY – STOCK STRUCTURE

Anthony Fowler

10.1 Introduction

The dispersion of individuals of a fish species usually conforms to an ensemble of local populations that constitutes a meta-population (Bailey 1997). Such local populations may be linked, to some extent, by the movement of individual fish. This could occur at either stage of the life history, i.e., by the transport of eggs and larvae associated with oceanographic processes, or the movement of juveniles and adults. The level of connectivity amongst local populations determines the extent to which the demographic processes that drive the population dynamics of adjacent populations are inter-related or independent of each other. Such connectivity, or lack thereof, determines the 'stock structure' of the meta-population. For fishery species, knowing the stock structure is important as it identifies the spatial scale at which significant demographic processes occur. This identifies the appropriate scale at which fishery assessment and management should be directed. In the past, failing to achieve this has led to notable failures in the single species approach to fishery management leading to fishery collapses (Stephenson 1999, Hutchinson 2008).

Determining the stock structure for marine fishery species is extremely challenging as it requires developing an understanding of the scale of fish movement and its demographic consequences potentially across complex oceanographic, inshore, and estuarine environments. Furthermore, the extent of such movement may vary temporally. Studies of stock structure have often been based on inferences about connectivity drawn from comparing genotypic and phenotypic characteristics amongst populations. Therein lies a further complexity in that such comparisons relate to evolutionary and ecological time scales, respectively. Because of the inherent challenges in comparing characteristics amongst populations, the process of determining stock structure could benefit from adopting a holistic or 'multiple technique' approach (Begg et al. 1999, Begg and Waldman 1999, Abaunza et al. 2008, Baldwin et al. 2012).

For Snapper throughout its Australian range, there have been numerous studies done at a variety of spatial scales that have contributed to the currently accepted understanding of stock structure (Fowler et al. 2021). It is apparent that there is an extensive range in the spatial scales over which stocks can be differentiated from the fine-scale stock structure that is evident in Shark Bay, Western Australia up to the extensive, cross-jurisdictional East Coast Stock that incorporates the populations of New South Wales and Queensland. For Snapper throughout the south-eastern geographic region of Australia that includes the regional populations of South Australia and Victoria, a comprehensive understanding of the life history and demography has been developed that has allowed strong inferences to be drawn about the connectivity amongst regional populations and the stock structure. The purpose of this chapter is to describe the chronology of studies that focussed on determining the stock structure and contributed to the current level of understanding to reveal how this understanding developed.

10.2 Materials and methods

Over the past 30 years in South Australia, there have been four studies that have focussed on determining the stock structure for Snapper. These involved either genetic or phenotypic comparisons amongst regional populations. Through this time, there were technological advancements in techniques that allowed the comparisons to become more comprehensive and sophisticated. The studies have culminated in a model of the demographic processes that drive the dynamics of the different regional populations, and the nature of connectivity between them, allowing strong inferences to be drawn about the stock structure. They have been summarised in several final reports and published papers. To show how understanding developed over time, the chronology of these studies was considered here by addressing several questions for each: when was the study done?; what was the fishery management context at the time and the primary issues being addressed?; what was the primary empirical approach that was used?; and what were the important findings that contributed to understanding connectivity amongst populations that led to conclusions about stock structure?

10.3 Results

10.3.1 1990s – mtDNA and allozyme markers

In the early 1990s, an FRDC-funded study (FRDC 94/168) considered the stock structure of Snapper across southern Australia (Donnellan and McGlennon 1996). At that time, the South Australian fishery was focussed in Northern Spencer Gulf (NSG). As such, the research focus, including commercial market sampling, was also focussed on this region (McGlennon and Jones 1997). However, the fishery was considerably more extensive than just this region as commercial and recreational fishing occurred throughout most of the State's coastal waters. Yet, the understanding of stock structure was insufficient to manage the fishery at this broad spatial scale (Donnellan and McGlennon 1996). Information was required on the number of stocks and their geographic distributions to determine their relative contributions to the State's catches and the rational allocation of fishing effort to each stock. Furthermore, such knowledge was required to ensure the integrity of the stocks if re-seeding was required. Prior to the study by Donnellan and McGlennon (1996), there was evidence for stock separation in the vicinity of the mouth of the Murray River between the populations of Victoria and south-eastern South Australia from those located further west (Sanders 1974, McDonald 1980). However, information on stock structure for populations west of the Murray mouth was ambiguous. Tag/recapture studies had suggested that the populations of Spencer Gulf and Gulf St. Vincent would likely be a single stock (Jones 1981, 1984), whilst the allozyme analyses of McDonald (1980) had suggested that fish from Spencer Gulf might be a discrete stock. The latter result was consistent with the fine-scale stock structure that was evident in Shark Bay, Western Australia, around that time (Johnson et al. 1986).

In the study of Donnellan and McGlennon (1996), data from mitochondrial DNA (mtDNA) and allozyme markers were compared amongst Snapper collected from 18 locations across southern Australia. These involved: one location in south-western Western Australia; eleven in South Australia located on the west coast and throughout Spencer Gulf, Gulf St. Vincent and Investigator Strait; and five locations distributed throughout Port Phillip Bay in Victoria. The samples were primarily collected in 1991 and 1992, but some were collected up to January 1996. Variation in mtDNA and at nine allozyme loci were examined at several scales, including whether there was more than one stock evident across the three main fishing areas of South Australia in Spencer Gulf, Gulf St. Vincent and the west coast of Eyre Peninsula.

The study confirmed a genetic division between Victorian and South Australian waters west of the mouth of the Murray River, consistent with earlier results from allozyme analysis (McDonald 1980) and tag/recapture data (Sanders 1974). However, for the Snapper populations of the two gulfs and the west coast, the data showed no significant differences in allele frequencies amongst populations. These results were consistent with the limited tag/recapture data that had demonstrated large-scale movement of adult Snapper such as between Spencer Gulf and

Investigator Strait (Jones 1981, 1984). The following hypothetical model relating to movement and connectivity was proposed for South Australian Snapper (Fig. 10.1) (McGlennon and Jones 1997, Fowler and Jones 2008). The model differentiated between groups of fish based on their movement behaviour. Of the juvenile fish that resulted from spawning in Spencer Gulf and Gulf St. Vincent, some subsequently remained in the gulfs and eventually supported the gulf-based fisheries, whereas others left the gulfs and migrated to the waters of the continental shelf. It was suggested that over years, such fish made annual spawning migrations back into the gulfs during which they were highly vulnerable to capture in the fishery. It was further suggested that by the age of ~12 years of age, the fish ceased this migratory existence and became permanent residents in the gulfs. This suggested that the migratory fish formed a mixed-age population on the continental shelf that was derived originally from age-related migration from different regions. It clearly provided opportunity for the mixing of fish from different origins including Spencer Gulf and Gulf St. Vincent, thereby accounting for the genetic homogeneity amongst populations located west of the mouth of the Murray River. This life history model was consistent with such Snapper populations, constituting a single, large, inter-mixed stock.

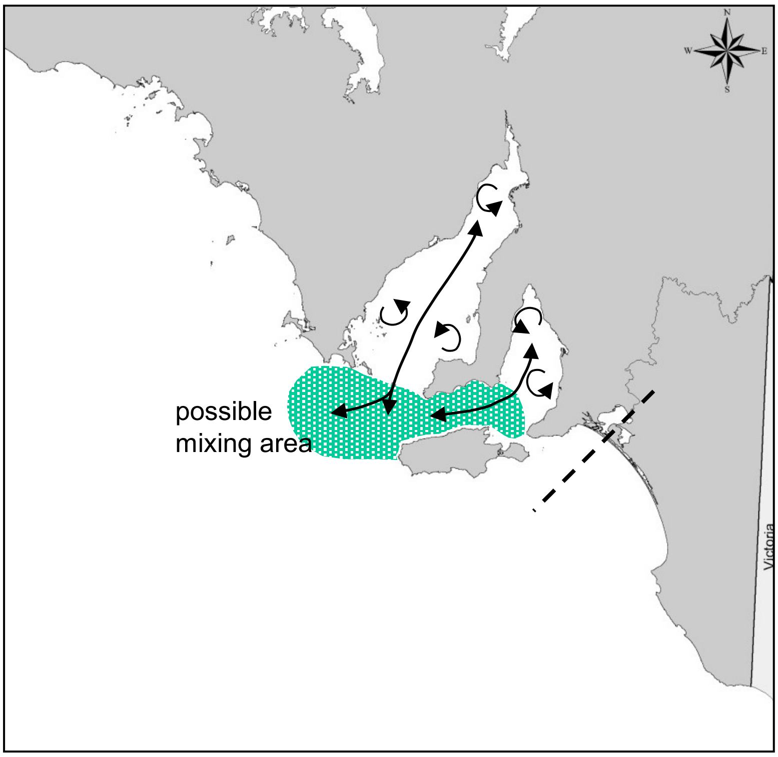

Fig. 10.1. The life history model developed during the 1990s from the genetic study by Donnellan and McGlennon (1996) and tag recapture data. The circular arrows represent within-region movement of ‘resident’ fish. The directed arrows show movement into and out of the gulfs by ‘migratory’ fish, and the proposed hypothetical mixing area for such fish on the continental shelf. The dashed line near the mouth of the Murray River represents the genetic division between populations to the east and west of this line.

10.3.2 early 2000s – otolith chemistry and population characteristics

The ensuing study on stock structure for Snapper in South Australia was also funded by FRDC (FRDC 2002/001) (Fowler et al. 2004). This project was developed during 2001, based on management issues that emerged throughout the late 1990s and early 2000s. These related to consistent poor fishery catches from Gulf St. Vincent that had crashed through the 1980s. Around 2000, the low catches from Gulf St. Vincent contrasted with record catches that were being taken from Spencer Gulf. At that time, these different regional trends in fishery catches were not consistent with the understanding of stock structure (Fig. 10.1), and the single-stock management strategy (McGlennon and Jones 1997). This led to the suggestion that managing the State-wide fishery might benefit from a regional approach that involved a stock rebuilding strategy in Gulf St. Vincent (McGlennon and Jones 1999). Yet, the limited understanding of the life history of Snapper meant that the likely consequences of a regional management approach were difficult to predict. Thus, it was apparent that there was a need for a comprehensive understanding of the movement patterns of Snapper, the connectivity amongst populations and the influence on stock structure.

This study addressed questions about the natal origins and connectivity amongst regional populations, based on the movement behaviour of Snapper and degree of ecological separation amongst regional populations (Fowler et al. 2004). The null hypothesis was that the South Australian Snapper population constituted a single, large stock that resulted from the mixing of individuals that were initially derived from different regions. Around 2000, the spatial scale of commercial market sampling had increased to include all six South Australian regions, which meant that, for the first time, data were available on fish size-at-age across the regional fisheries (Fowler 2002, Fowler et al. 2004). This meant also that the archive of Snapper otoliths that was accumulating from such sampling, involved otoliths from fish that were sampled from the same year classes and ages but from different regions. This stock structure study utilised this by undertaking a regional comparison of the chemistry of otoliths of nine-year-old fish that had been sampled in 2000 and had recruited as 0+ fish as part of the strong 1991-year class (Fowler et al. 2004, 2005). As such, the otoliths considered were from fish that were the same age and had lived through the same period. This, thereby, removed temporal differences as a potential confounding factor for the regional comparison. Whole otoliths from similar-aged fish from different regions were considered using solution-based inductively coupled plasma mass spectrometry (ICPMS). Also, TS-sections of otoliths were analysed with laser ablation ICPMS providing age-related profiles of elemental concentration (Appendix 10.6.1, Fowler et al. 2004, 2005). Also, the spatially broad commercial market sampling allowed for the development of region-specific estimates of population size and age structures and demographic parameters (Fowler et al. 2004). The regional comparison of these augmented the spatial comparisons of the otolith chemistry datasets.

The study determined that the elemental concentrations in otoliths did vary regionally, thereby revealing significant regional sub-structuring (Appendix 10.6.1, Fowler et al. 2004, 2005).

Furthermore, population size and age structures and demographic characteristics, including growth rates, also differed amongst regions. Such spatial differences in several phenotypic characteristics meant that for considerable periods of their lives, Snapper that lived in the different regions of South Australia's coastal waters must have experienced different environmental conditions. For the first time, this indicated a level of ecological separation amongst regional populations. This was a significant finding that was not consistent with the South Australian Snapper population being a single, large inter-mixed population.

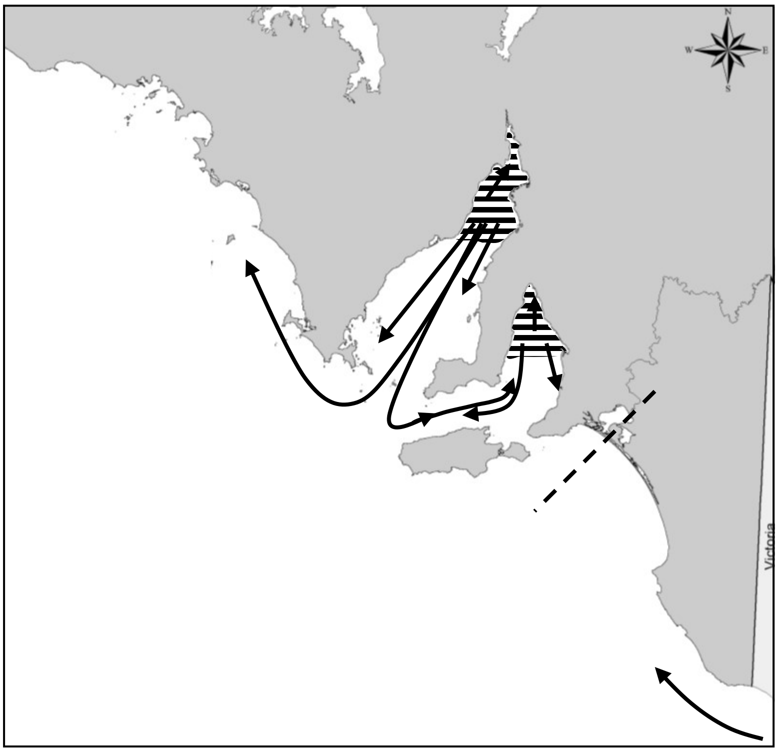

Fig. 10.2. The proposed dispersion of Snapper based on the movement of fish, from the results of otolith chemistry analysis (Fowler et al. 2004, 2005). Proposed nursery areas are located in the northern gulfs, from which fish disperse to other regions when 3-5 years old. The dashed line near the mouth of the Murray River represents the genetic division between populations to the east and west of this line.

The age profiles of elemental concentrations determined by laser ablation ICPMS provided significant insights into the life histories of adult Snapper (Fowler et al. 2005). The study identified that the regional differences in otolith chemistry were related to age, i.e., for the three annual increments that related to the first three years of the fishes' lives there were virtually no differences amongst regions, compared with the later formed ones when the fish were older (Appendix 10.6.1). This initial similarity amongst regions in otolith chemistry for the young fish was interpreted in terms of the natal origins of the fish. It was inferred that adult fish that were sampled from different regions had a common origin and had spent the first three years of their lives in the same region. At the time, it was speculated that NSG was the region that supported such important natal nursery areas (Fig. 10.2), from the results of prawn by-catch surveys and juvenile Snapper surveys (Chapter 6).

Also, there was evidence that Northern Gulf St. Vincent (NGSV) may also have been an important nursery area (Chapter 6).

From around the age of three years onwards, the age-related otolith chemistry profiles for the different regions diverged and remained separate (Appendix 10.6.1, Fowler et al. 2004, 2005). These divergences were consistent with many fish leaving the vicinity of the nursery areas, moving considerable distances, and joining populations that were living in adjacent regions. These fish then largely remained resident to these regions where, by four years of age, they contributed to the fishery catches. Throughout the 1990s, every South Australian regional population experienced increases in biomass associated with the exceptional 1991-year class, evident as increases in catches and catch rates.

Based on the life history model that emerged from this study (Fig. 10.2), the Snapper populations that occupied NSG and possibly also NGSV were the source populations for a number of sink populations located in adjacent regions (Fowler et al. 2004). The replenishment of the populations in the latter regions resulted from age-related movement over distances of up to hundreds of km. This model proposed that rather than being a single, large, mixed stock, the South Australian population of Snapper was composed of numerous, ecologically separated sub-populations that originated in one or two primary nursery areas. Such a model of regional sub-structure and replenishment accounts for how the regional populations demonstrated ecological separation that was evident as differences in phenotypic characteristics but nevertheless did not show evidence of genetic differentiation (Donnellan and McGlennon 1996).

10.3.3 late 2000s – otolith chemistry and population characteristics

The following study that considered the stock structure of Snapper throughout south-eastern Australia was undertaken approximately a decade later. This was another FRDC-funded study (FRDC 2012/020), that was conceived and developed through 2011 for funding from 2012 onwards for which the empirical data were collected from then until 2015. The need for the project was based on management concerns that developed during the first decade of the 2000s (Fowler 2016, Fowler et al. 2013, 2016, 2017). The first concern related to a dramatic switch that had occurred in the commercial fishery primarily from the use of handlines to new longline fishing technologies. This increased the effectiveness of fishers, resulting in higher targeted fishing effort and catch rates (Fowler et al. 2020). Concomitantly there was a dramatic change in the spatial structure of the fishery. Prior to 2003, the relatively small region of NSG had generally contributed >50% of the State's annual catches, whilst for a few following years, Southern Spencer Gulf (SSG) had dominated the catches. However, from 2007 onwards, the combined annual catches from NSG and SSG declined, dropping to low levels in 2012 and subsequently remaining low (Fowler et al. 2013, 2016, 2020). Concomitantly, there were exponential increases in catches and catch rates in several other regions, notably NGSV and the southeast region (SE-Region). Between 2007 and 2012, the declines in catches from Spencer Gulf was a warning about the long-term sustainability of the fishery in NGSV, given the record levels of longline catch, effort and CPUE that were being recorded for that region at that time.

Despite the advances in understanding about the life history and stock structure that were made in the previous study (Fowler et al. 2004), it was still apparent that the processes that underpinned the recent changes in the spatial structure of the fishery were not understood. For the different regional populations, it was necessary to provide more certainty about the natal origins of the fish and their subsequent movement patterns. This project addressed such questions about connectivity at several spatial and temporal scales. It was based on the regional comparison of phenotypic characteristics, similar to the previous study (Fowler et al. 2004). It involved another otolith chemistry study that provided comparative, age-related data amongst regions that were interpreted in terms of the natal origin and inter-regional movement of fish throughout their lives. This was augmented with comparative demographic data that included population size and age structures.

This new otolith chemistry study was done in collaboration with Fisheries Victoria using a similar approach to the earlier study (Fowler et al. 2004), whereby the chronological structure of the TS-sections of the otoliths were sampled for elemental concentrations using LA-ICPMS. This time, the otoliths from four year-classes were considered, i.e., 1991, 1997, 2001 and 2004, which were relatively strong year classes in at least some regions (Chapter 9). The otoliths had previously been collected from fish sampled from five South Australian regions of NSG, SSG, NGSV, SGSV and the SE-Region as well as from Port Phillip Bay (PPB), Victoria. The resulting age-related profiles of concentrations of barium, strontium, manganese and magnesium were compared and interpreted in terms of where fish had originated and inter-regional movement, providing insights into connectivity and stock structure (Appendix 10.6.2).

This study was the beneficiary of important research that was undertaken in Victoria throughout the 2000s. That work was based on detailed otolith chemistry studies during which it was discovered that the otoliths of Snapper from PPB, have elevated levels of Ba, reflecting high ambient levels in the waters of this bay (Hamer et al. 2003, 2005, 2006). So, the Ba concentrations in otoliths constituted an important natural tag with which to differentiate fish from PPB from those from outside the bay. Such work had already identified that PPB is a primary spawning ground and nursery area that is the primary source of replenishment for Snapper populations located along the west coast of Victoria (Hamer et al. 2006, 2011).

The regional comparison of age-related estimates of elemental concentrations from the five South Australian regions and PPB, provided compelling results from which processes of inter-regional movement were inferred (Appendix 10.6.2). The results for the 2001-year class showed the strongest regional differences against which those for the 1991, 1997 and 2004-year classes were compared (Appendix 10.6.2, Fowler et al. 2017). For the otoliths from the 2001-year class from

PPB, SE-Region and SGSV, the elemental concentrations were similar for the first four increments, but subsequently diverged. From this, it was inferred that these fish had originated in PPB, before some migrated from the bay and moved westwards, some reaching the SE-Region and Cape Jervis in SGSV. This result informed about the westward extent of the movement of Snapper that had originated in PPB (Hamer et al. 2011). For the SE-Region, the otoliths from the 2004-year class gave similar results to those of the 2001-year class. From this, it was evident that the episodic productivity of the fishery in the SE-Region related to mass emigration of juvenile/sub-adult fish from PPB and their age-related movement over 600 km to this region over 3 – 5 years.

The results for the 2001-year class from SGSV (sampled in the vicinity of Cape Jervis), indicated that these fish had also originated in PPB. In contrast, those from the 2004-year class that were sampled from the same region had elemental concentrations that were similar to those from NSG and NGSV, indicating that they had not originated in PPB. The results for the 1991 and 1997-year classes also excluded PPB as their natal source. For the latter year class, the elemental concentrations were more consistent with those for NSG, suggesting that this region was the likely natal source. For SGSV, the results from different year classes indicated that this region was a mixing zone for Snapper that had originated in different nursery areas.

For the 2001-year class, the elemental concentrations for otoliths from NSG, NGSV and SSG indicated that the Victorian fish did not extend into Spencer Gulf or Gulf St. Vincent. Rather, these fish were likely to have originated in the nursery areas of NSG and/or NGSV. Those from SSG most likely originated in NSG and moved southwards during their 3rd year onwards. For NGSV, the processes involved in the significant increase in biomass that occurred through the 2000s, may have involved emigration of fish from NSG, or regionally independent processes of reproduction and recruitment (Fowler et al. 2017). Differentiating between these hypotheses, based only on the otolith chemistry results, was difficult. However, there were several other datasets and considerations that were consistent with the second hypothesis (Fowler et al. 2017).

10.3.4 late 2000s - genomics

The most recent study that considered the stock structure of Snapper in south-eastern Australia was that by Bertram et al. (2023). This was part of the ARC-funded project ‘Fisheries genomics of Snapper in Australian and New Zealand waters’ (Project LP180100756), a genetic study based on the analysis of large datasets for genome-wide single nucleotide polymorphisms (SNP). Such SNP datasets are powerful at detecting subtle genetic structure, which is common for marine species, thereby increasing the value of such genetic studies.

A total of 488 Snapper that were sampled from 11 localities across south-eastern Australia provided useful information on genomic structure. These localities included: six that were located in South Australia, i.e., Ceduna (CED), NSG, SSG, NGSV, SGSV, Kingston/SE (KSE); four in Victoria, i.e., Portland (PLD), PPB, Westernport Bay (WPB), and Lakes Entrance (LE); as well as Eden (EDN), which is located in southern NSW. A total of 10,916 single SNPs were used to assess genomic differentiation that could be related to coastal biogeography. At the broad geographic scale, the population structure was predominantly shaped by two genetic discontinuities located: in the vicinity of the mouth of the Murray River; and the Victorian/NSW border. These divided the populations into three clusters of genomic structure that were identified as a South Australian Stock that involved the samples from CED, NSG, SSG, NGSV and SGSV; a Victorian Stock included the samples from KSE, PLD, PPB, WPB and LE; and the NSW stock involved the sample from EDN. The three clusters corresponded to the boundaries of the three biogeographic provinces of south eastern Australia, i.e., Flindersia, Maugea and Peronia (Fig. 10.3).

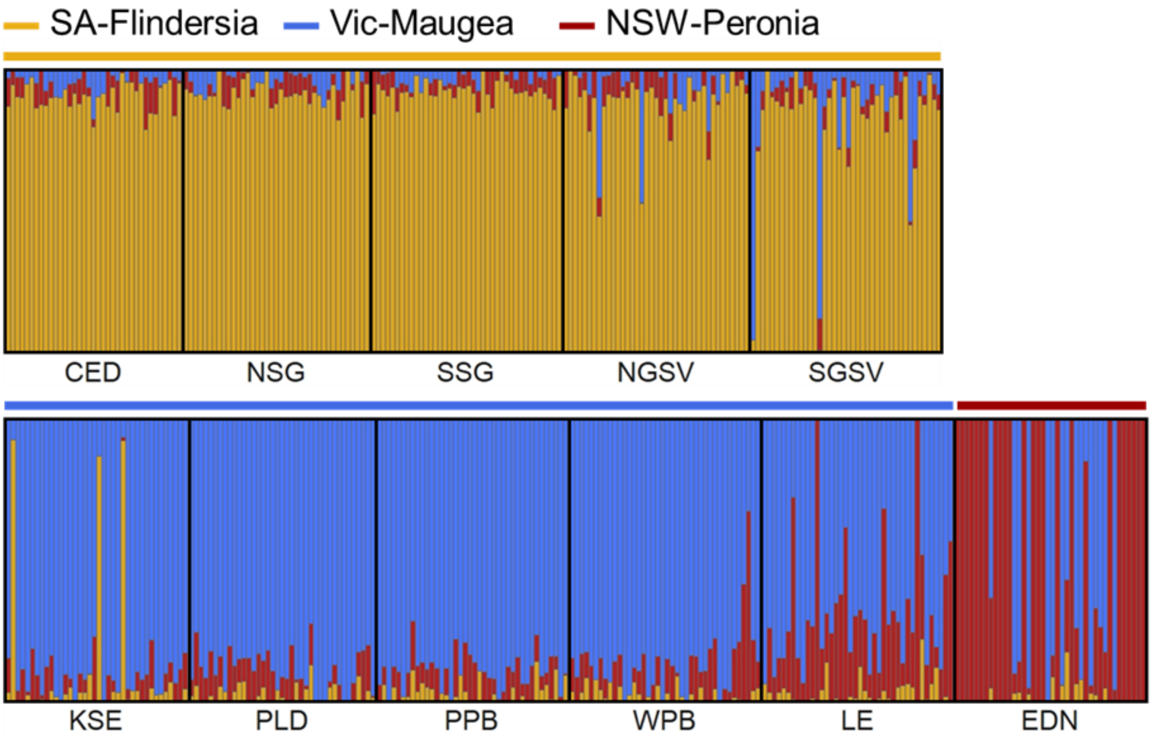

Fig. 10.3. Figure copied from Bertram et al. (2023), showing the results from the genomics study involving 432 Snapper and 10,916 neutral SNPs. Each vertical bar shows the genotype of an individual. The colour shows the probability of membership to each of the three groups by its colour makeup. Biogeographic provinces (Flindersia, Maugea, Peronia) and genetic groupings (SA, Vic, NSW groups) are marked above the plots.

A further significant finding of this study was that there was evidence of some migration between the adjacent putative stocks (Fig. 10.3). For SGSV, i.e., part of the South Australian Stock, there were two migrants from Victoria as well as several individuals with mixed ancestry. No such migrants were evident for NSG, SSG or CED. There were also three migrants from South Australia that were detected in the sample from KSE, but none further east in PLD, PPB or WPB. The less obvious genetic differentiation between the Victorian and NSW samples suggested that dispersal between them was more bi-directional and frequent, including north-eastward movement against the East Australian Current. The sample from LE contained migrants from NSW and individuals with mixed ancestry. WPB was the most western Victorian sample that involved individuals with considerable NSW ancestry. The sample from EDN predominantly involved individuals with NSW ancestry, but also included fish that were migrants from Victoria and others with mixed ancestry. Whilst the genetic break between the South Australian and Victorian samples was quite abrupt, there was considerably more overlap between the Victorian and NSW samples, suggesting that a region of isolation by distance may occur between them.

This genetic study involved a temporal component whereby the consistency in genetic structure was compared between samples collected in 2010 and those collected in 2018 and 2019 (Bertram et al. 2023). The samples considered in these temporal comparisons were collected from NGSV, Victoria and NSW. The results indicated stability in population genetic structure over periods of eight and nine years. In 2010, one Victorian migrant detected in NGSV, indicated the consistency in the migration process over this spatial scale.

Spatial auto-correlation analysis was also done which identified the spatial scales over which individuals were more genetically similar than expected at random (Bertram et al. 2023). Genomic variation was non-random for the South Australian and Victorian Stocks, indicating some genetic sub-structuring amongst localities in the same stocks. The autocorrelation coefficients were highest for NSG, NGSV, LE and EDN, but were not significant for SSG, PLD and WPB. In South Australia, there was genetic differentiation between samples from GSV (especially NGSV), SG and CED. At the within-locality scale, individuals were most similar at both NSG and NGSV, potentially the two most important spawning and nursery areas for South Australian populations. These results are consistent with the lack of mixing between the gulfs during both life history stages, suggesting local recruitment processes and the site fidelity of juvenile and adult fish.

10.4 Discussion

The stock structure of a metapopulation of a fish species depends on the connectivity amongst the component populations. This reflects the spatial extent of fish movement, the numbers of fish that move relative to population abundances and the influence that such movement has on the demographic processes and population dynamics of local populations. For Snapper in south-eastern Australia over the past 30 years, there has been significant progress in understanding these issues. Such progress has resulted from studies that have contributed to understanding the population biology of the species, including those focussed on stock structure that were considered in this chapter. The latter included two genetic studies, one done during the 1990s and the second in the late 2000s, that compared genotypic data amongst samples from populations collected across the geographic region. The other two studies, done during the early and then later 2000s, compared phenotypic characteristics amongst regional populations. Here, the value of age-related data from TS-sections of otoliths determined using laser ablation ICPMS cannot be over-stated, as they informed about the natal origins of fish and the timing of subsequent inter-regional movement. Overall, the genetic and phenotypic results informed about the natal origins of fish, movement between regions and their consequences for stock structure.

10.4.1 1990s – mtDNA and allozyme markers

During the early 1990s, understanding of the population biology of Snapper in south-eastern Australia was emerging based on commercial market sampling, the ageing of adult fish and tag/recapture studies. In this context, the first genetic study that considered mtDNA and allozyme frequencies, produced two important findings (Donnellan and McGlennon 1996). The first was recognition of a genetic division around the mouth of the Murray River between Victorian and South Australian populations. Whilst now considered a highly important finding, at that time the lack of a significant fishery in the SE-Region of South Australia meant that there was little need to further explore the nature of this putative stock division. The second finding was that it recognised genetic homogeneity amongst the remaining South Australian populations, including those in Gulf St. Vincent, Spencer Gulf and the west coast of Eyre Peninsula. This was considered a consequence of the movement capabilities of the fish as determined from tag/recapture studies (Jones 1981, 1984). The results were interpreted as the populations located west of the Murray mouth constituting a single, large, inter-mixed stock (Fig. 10.1).

10.4.2 early 2000s – otolith chemistry and population characteristics

In the early 2000s, the second stock structure study primarily focussed on inter-regional comparisons of phenotypic characteristics for fish from the 1991-year class, an exceptionally strong year class for most South Australian regional populations. There were two important findings of this study (Fowler et al. 2004, 2005). It revealed, for the first time, that the South Australian regional populations did display considerable sub-structuring, indicative of some ecological separation amongst them. Secondly, the otolith chemistry study indicated that such regional differences were not consistent throughout the fishes' lives but were related to age. For the first three years of their lives, the regional differences were either non-existent or slight, but became more evident from the approximate age of three years onwards, remaining evident throughout the older years. From these results were developed the concepts of 'primary nursery areas' and age-related, inter-regional migration of large numbers of fish over distances of up to hundreds of km. The revised life history model shown in Fig. 10.2 was developed. Given that, at the time, this model was contrary to the single stock concept, there remained some uncertainty about it and its consequences for stock structure. As such, the findings of this first otolith chemistry study were not fully appreciated until later when reconsidered in the context of those from later studies done in Victoria (Hamer et al. 2005, 2006, 2011) and South Australia (Fowler et al. 2016, 2017).

10.4.3 late 2000s – otolith chemistry and population characteristics

The Victorian studies referred to above were largely done in the period between the first and second otolith chemistry studies in South Australia. They recognised that PPB was an important primary nursery area for Snapper from which emigration was the primary source of replenishment for populations located along the western coast of Victoria. The processes here were very similar to the model of population replenishment (Fig. 10.2) that was proposed above for the regional South Australian populations (Fowler et al. 2004, 2005). The later project by Fowler (2016), then extended the findings of the Victorian studies. It indicated that migrants from PPB travelled even further westward and replenished the population of the SE-Region of South Australia, with some fish reaching as far west as Cape Jervis in SGSV. Ultimately, this project led to the significant conceptual advancement that the episodic nature of the population dynamics and fishery production for the SE-Region related to inter-annual variation in recruitment to PPB, and the migration to this region over approximately 600 km of what must have been hundreds of thousands of Snapper. This conclusion about replenishment of the population of the SE Region was largely based on the fortuitous, clear elemental fingerprint in the otoliths of fish that originated in PPB (Hamer et al. 2005, 2006), but was also consistent with other findings such as population age structures and the results from recruitment surveys in PPB (Fowler et al. 2017).

For the other South Australian regions west of the Murray mouth, it was evident from otolith chemistry results and population age structures that similar demographic processes occurred. NSG was an important primary nursery area (Chapter 6) that supported a population of relatively high biomass and displayed considerable variation in age class strength, reflecting significant inter-annual variation in recruitment (Chapter 9). Other regions such as SSG, Investigator Strait and the west coast of Eyre Peninsula, were sink populations to which fish from NSG eventually migrated. There was also evidence of a further primary nursery area in NGSV, which likely led to replenishment of the population in SGSV.

From this project was developed the following meta-population model for the geographic region of south-eastern Australia (Fowler et al. 2016, 2017) (Fig. 10.4). Two primary nursery areas were recognised, i.e., NSG in South Australia and PPB in Victoria, with some evidence for a third nursery area in NGSV (Fowler 2016). These regions sustained source populations of Snapper from which some fish emigrated to sink populations in adjacent and distant regions. The age structures of the populations in such regions reflected the consequence of significant inter-annual variation in recruitment (Chapter 9). Several years after recruitment of a strong year class, some fish emigrated from the natal regions, and dispersed over distances of up to hundreds of km, invading and replenishing the populations in adjacent regions. In contrast, when recruitment year classes were weak, then no or very little such fish movement could have occurred. As such, regional populations have been replenished through density dependent, age-related migration of fish at rates determined by recruitment variability in the primary nursery areas. Given the low frequency of strong recruitment year classes for NSG (Chapter 9), it is likely that significant inter-regional movement and population replenishment has occurred only occasionally. Such recruitment events were separated by periods of years of poor recruitment that resulted in low rates of emigration to and replenishment of sink populations. Despite such periods of ecological separation, the inter-regional movement associated with the occasional strong year class was sufficient to maintain genetic homogeneity.

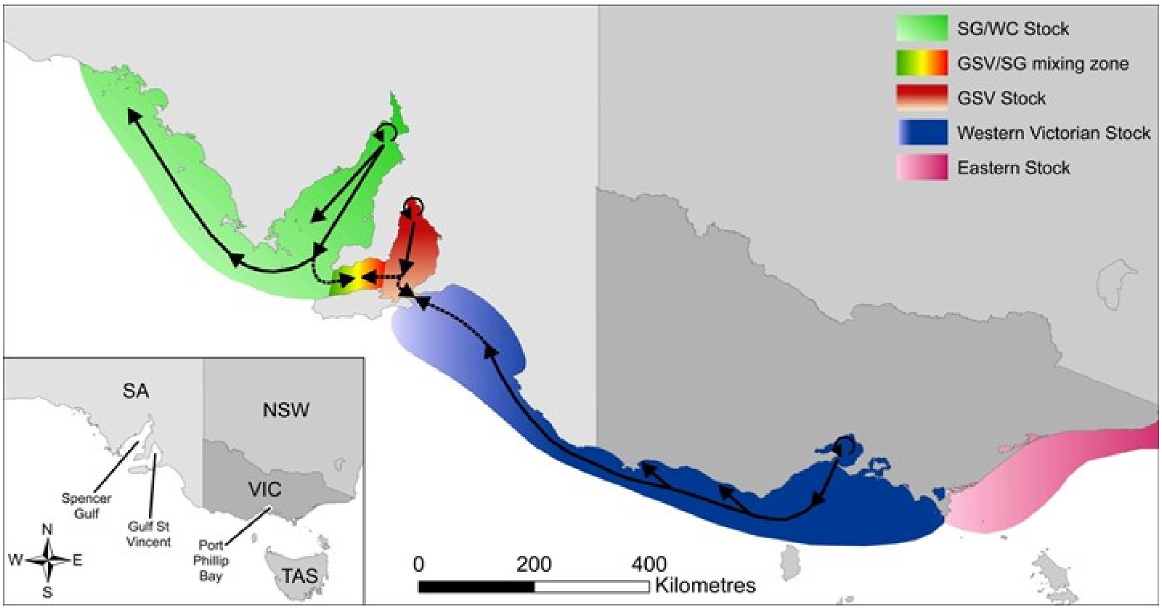

Fig. 10.4. Map of south-eastern Australia showing the putative stock structure that was developed from the stock structure studies. It shows the three stocks that occur in South Australian waters. The arrows show the movement patterns of Snapper inferred from otolith chemistry studies.

From the connectivity amongst regional populations, it was proposed that there are three stocks that occur, at least partly, in South Australian waters (Fig. 10.4) (Fowler et al. 2016, 2017): the population in the SE-Region represents the western extent of the Western Victorian Stock that is based around the primary nursery area and source population of PPB; the Spencer Gulf/West Coast

Stock includes the populations of NSG, SSG and the WC of Eyre Peninsula, and is dependent on the primary nursery area in NSG; the Gulf St. Vincent Stock, which includes the regional populations of NGSV, SGSV including Investigator Strait. It is likely that the boundary areas of the different stocks overlap, with mixing of individuals from different natal origins. Overall, the different regional trends in population dynamics reflected different temporal trends in recruitment to the three primary nursery areas that determined the rates of and spatial extent of emigration to adjacent regions. These are considered in more detail in Chapter 12 to account for the recent regional trends in population dynamics.

10.4.4 late 2000s - genomics

The genomics study (Bertram et al. 2023) was done several years after the otolith chemistry studies (Fowler et al. 2017). It used a different technological approach but provided findings that were largely consistent with the earlier ones, thereby providing significant validation for the proposed model in Fig. 10.4. It identified a significant genetic discontinuity in south-eastern South Australia between essentially the Victorian and South Australian populations. This finding clearly confirmed the division that had been proposed from earlier tag/recapture work (Sanders 1974), genetic data (Donnellan and McGlennon 1996), and otolith chemistry analyses (Fowler et al. 2017). It was consistent with the putative division between the Western Victorian Stock and the proposed South Australian stocks (Fowler et al. 2017).

The genomics study also recognised small-scale differences in genetic structure between some regions such as NSG and NGSV. Such differences are consistent with there being some ecological separation between regional populations, consistent with the lack of mixing of larvae and the site fidelity of adult fish. Those fish whose DNA was considered were not from a strong year class in Spencer Gulf, suggesting that they are unlikely to have undertaken large-scale, density dependent migration. Such proposed ecological separation of populations amongst regions is consistent with the results from the earlier otolith chemistry and morphological studies (Rogers 2014).

There was one further important finding of the genomics study that was apparent in the visual representation of the genotypes of the individual fish (Fig. 10.3) (Bertram et al. 2023). The comparison of these clearly demonstrated the relative genetic homogeneity of the regional populations from the South Australian gulfs and the west coast of Eyre Peninsula, and the clear genetic differentiation from the sample considered from KSE. Nevertheless, these data also demonstrated clear migrants between regional populations. Several Snapper from SGSV had genotypes that were consistent with the Western Victorian Stock. Also, there were fish that were genetic hybrids located in NGSV. Such migrants and hybrids were not evident in the samples from NSG, SSG or CED. Similarly, there were three fish whose genotypes were typical of the gulfs that were included in the KSE samples. These observations are consistent with the movement of some individuals across the putative boundary between the SE-Region and the SGSV. This supports the suggestion made above for SGSV that some areas are mixing zones for fish that originate from different nurseries, and so would be recognised as belonging to different putative stocks.

10.5 References

Abaunza, P., Murta, A.G., Campbell, N., Cimmaruta, R., Comesana, A.S., Dahle, G., Garcia, Santamaria, M.T., Gorod, L.S., Iversen, S.A., MacKenzie, K., Magoulias, A., Mattiucci, S., Molloy, J., Nascetti, G., Pinto, A.L., Quinta, R., Ramos, P., Sanjuan, A., Santos, A.T., Stransky, C., Zimmermann, C. (2008). Stock identity of horse mackerel (*Trachurus trachurus*) in the northeast Atlantic and Mediterranean Sea: integrating the results from different stock identification approaches. Fisheries Research 89: 196-209.

Bailey, K.M. (1997). Structural dynamics and ecology of flatfish populations. Journal of Sea Research 37: 269-280.

Baldwin, R.E., Banks, M.A., Jacobson, K.C. (2012). Integrating fish and parasite data as a holistic solution for identifying the elusive stock structure of Pacific sardines (*Sardinops sagax*). Reviews in Fish Biology and Fisheries 22: 137-156.

Begg, G.A., Friedland, K.D., Pearce, J.B. (1999). Stock identification and its role in stock assessment and fisheries management: an overview. Fisheries Research 43: 1-8.

Begg, G.A., Waldman, J.R. (1999). An holistic approach to fish stock identification. Fisheries Research 43: 35-44.

Bertram, A., Bell, J., Brauer, C., Fowler, A., Hamer, P., Sandoval-Castillo, J., Stewart, J., Wellenreuher, M., Beheregaray, L. (2023). Biogeographic provinces and genomically-delineated stocks are congruent in Snapper (*Chrysophrys auratus*) from south-eastern Australia. ICES Journal of Marine Science. (in press).

Donnellan, S.C., McGlennon, D. (1996). Stock identification and discrimination in Snapper (*Pagrus auratus*) in southern Australia. Final Report to FRDC. 31pp.

Fowler, A.J. (2002). Snapper (*Pagrus auratus*). Fishery assessment report to PIRSA for the Marine Scalefish Fishery Management Committee. South Australian Fisheries Assessment Series 01/013. 64 pp.

Fowler, A.J. (2008). The population biology of Snapper (*Chrysophrys auratus*) in Gulf St. Vincent. In: Shepherd, S.A., Kirkegaard, I., Harbison, P., and Jennings, J.T. (eds). Natural history of Gulf St. Vincent. Royal Society of South Australia Inc. pp 385-398.

Fowler, A.J. (ed) (2016). The influence of fish movement on regional fishery production and stock structure for South Australia's snapper (*Chrysophrys auratus*) fishery. Final report to FRDC (Project No. 2012/020). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 181 pp.

Fowler, A.J., 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., Hall, K.C. (eds) (2004). Adult migration, population replenishment and geographic structure for snapper in SA. Final report to FRDC (Project No. 2002/001). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication Number RD04/0163. 152 pp.

Fowler, A.J., Gillanders, B.M., Hall, K.C. (2005). 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, R., Burch, P., Feenstra, J.E., Jackson, W.B., Lloyd, M. (2013). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-3, SARDI Research Report Series No. 713. 103pp.

Fowler, A.J., McGarvey. R., Carroll, J., Feenstra, J.E., Jackson, W.B., Lloyd, M.T. (2016). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-4. SARDI Research Report Series No. 930. 82pp.

Fowler, A.J., Hamer, P.J., Kemp, J. (2017). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely-dispersed, coastal fishery species. Fisheries Research 189: 77-94.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

Fowler, A., Stewart, J., Victorian Fisheries Authority, Roelofs, A., Garland, A., Jackson, G. (2021). Snapper (*Chrysophrys auratus*), in Toby Piddocke, Crispian Ashby, Klaas Hartmann, Alex Hesp, Patrick Hone, Joanne Klemke, Stephen Mayfield, Anthony Roelofs, Thor Saunders, John Stewart, Brent Wise and James Woodhams (eds) 2021, Status of Australian fish stocks reports 2020, Fisheries Research and Development Corporation, Canberra.

Hamer, P.A., Jenkins, G.P., Gillanders, B.M. (2003). Otolith chemistry of juvenile Snapper *Pagrus auratus* in Victorian waters: natural chemical tags and their temporal variation. Marine Ecology Progress Series 263: 261-273.

Hamer, P.A., Jenkins, G.P., Gillanders, B.M. (2005). Chemical tags in otoliths indicate the importance of local and distant settlement areas to populations of a temperate sparid, *Pagrus auratus*. Canadian Journal of Fisheries and Aquatic Sciences 62: 623-630.

Hamer, P.A., Jenkins, G.P., Coutin, P. (2006). Barium variation in *Pagrus auratus* (Sparidae) otoliths: a potential indicator of migration between an embayment and ocean waters in south-eastern Australia. Estuarine, Coastal and Shelf Science. 68: 686-702.

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Hutchinson, W.F. (2008). The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. Biological letters 4: 693-695.

Johnson, M., Creagh, S., 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.K. (1981). Biological research on snapper (*Chrysophrys auratus* syn. Unicolor) and an analysis of the fishery in Northern Spencer Gulf. SAFISH 5-8.

Jones, G.K. (1984). A review of the commercial fishery for snapper (*Chrysophrys auratus*) in South Australian waters. Discussion paper, Department of Fisheries, South Australia. November 1984.

McDonald, C.M. (1980). Biochemical, genetic and systematic studies of *Arripis* and *Chrysophrys* fish species. Unpublished PhD thesis. Australian National University.

McGlennon, D., Jones, K. (1999). Snapper (*Pagrus auratus*). Fishery assessment report to PIRSA for the Marine Scalefish Fishery Management Committee. South Australian Fisheries Assessment Series 99/13. 23 pp.

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.

Stephenson, R.L. (1999). Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fisheries Research 43: 247-249.

10.6 Appendices

10.6.1 Regional comparison of otolith chemistry for the 1991-year class

This appendix reviews and summarises the results and findings from two significant otolith chemistry studies that have been done for adult Snapper in South Australia (Fowler 2016, Fowler et al. 2004, 2005, 2017). The first study was undertaken during the early 2000s as part of FRDC Project 2002/001 (Fowler et al. 2004, 2005). There were several components that involved different analyses of otolith chemistry. These used either solution-based inductively coupled plasma mass spectrometry (ICPMS) to quantify elemental concentrations of whole otoliths (Chapter 5 in Fowler et al. 2004), or laser ablation ICPMS to provide age-related estimates of elemental concentrations across the chronological structure of the transverse sections of the otoliths (Chapters 3, 6 in Fowler et al. 2004). Each component was done for similar-aged Snapper from the different regions around South Australia. The purposes were to interpret the elemental concentrations in terms of the natal origins and the likely movements of fish between regions throughout their lives.

This otolith chemistry study focussed on Snapper in the 9+ age class from the 1991-year class that had been sampled in 2000 (Fowler et al. 2005). Otoliths from six regions of marine waters were considered, i.e., WC, NSG, SSG, NGSV, SGSV and the SE. These regions differed considerably in their SST and salinity regimes as well as the physical oceanographic processes that would likely impact on ambient elemental concentrations. Transverse sections of the otoliths were prepared, and then sampled across their chronological structure with laser ablation ICPMS providing profiles of elemental concentrations for ^{138}Ba and ^{88}Sr (Appendix in Fowler et al. 2004). These profiles were summarised by calculating age-related estimates of the concentrations for both elements, which were then compared amongst the regions (Fowler et al. 2004). Furthermore, the increment widths were measured across otoliths and considered in the inter-regional comparisons.

A second component of the otolith chemistry study that was done during the early 2000s, used laser ablation ICPMS to focus on the natal origins of Snapper from the six regional populations (Chapter 6 in Fowler et al. 2004). Here, the trace element composition of the cores of the otoliths were sampled, relating to the larval and early juvenile phase of the life history. The same otoliths that were considered for the otolith chronology study were also considered here.

The final component of the suite of otolith chemistry studies done during the early 2000s used solution-based ICPMS on whole adult Snapper otoliths (Chapter 5 in Fowler et al. 2004). Here, again, otoliths from the 1991-year class were considered from the six regions. These fish were in the 11+ age class having been sampled in 2002. Since, the estimates of elemental concentration were integrated across the whole lifetime of each fish, the final results were the consequence of different environments that each had lived in during its life. Age-related data were not available for this component.

Inter-regional variation in age-related profiles

For each of the parameters of increment widths (IncW), ^{88}Sr and ^{138}Ba there were significant age-related regional differences. The regional differences in IncW related to the two northern gulfs having higher mean increment widths for increment numbers 4 to 9 compared to the other four regions (Fig. A10.1), indicating spatial differences in the development of the otoliths. For ^{138}Ba, the regional differences also only related to the 4th to 9th increments from the otolith core. Again, these related to differences between the northern and southern gulfs. For ^{88}Sr, the age-related differences amongst regions again involved increment numbers 4 to 9, which particularly related to differences between NSG, NGSV and SSG from the other three regions. No such regional differences were apparent for the first three annual increments.

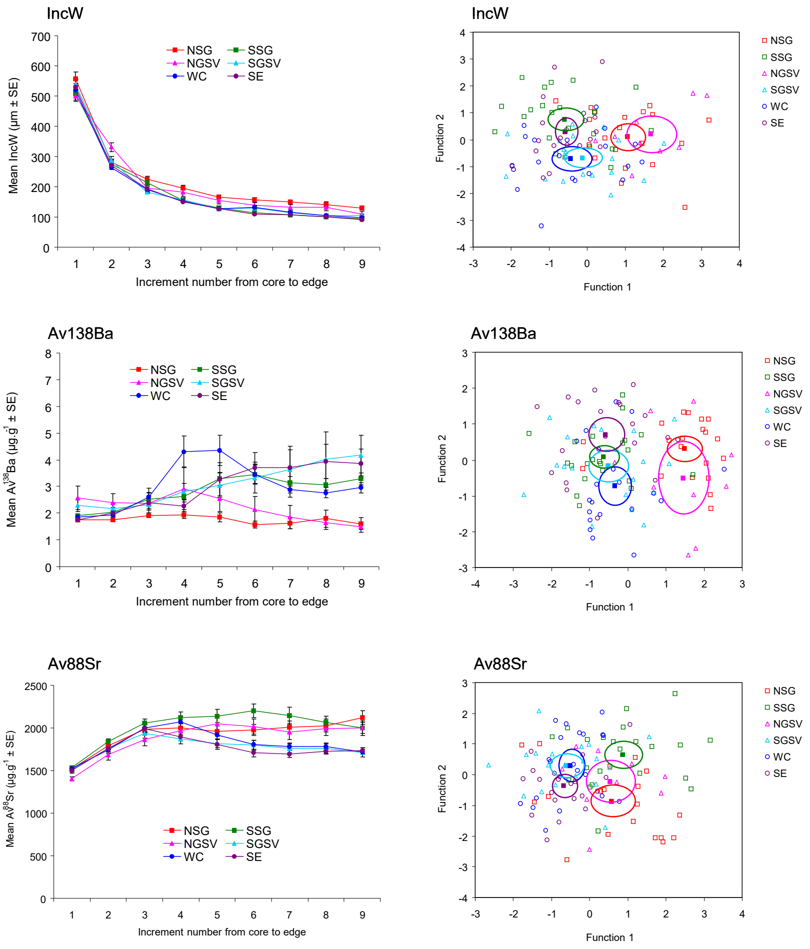

Fig. A10.1. Profiles and results from step-wise discriminant function analyses for the mean values of IncW, Av88Sr and Av138Ba for the nine increments from the core to the outer edge of the otolith sections for each geographic region.

The data for the three variables of Av88SR, Av138Ba and IncW were considered together in multivariate analyses for each of the nine increments separately (Fig. A10.2). For the first three increments there was little inter-regional variation. Only NGSV separated from the other five regions for which the centroids and 95% confidence limits largely overlapped. However, for the 4th to 9th increments, significant variation was apparent. In particular, the estimates for NSG and NGSV separated from the more southern regions (Function 1 in Fig. A10.2).

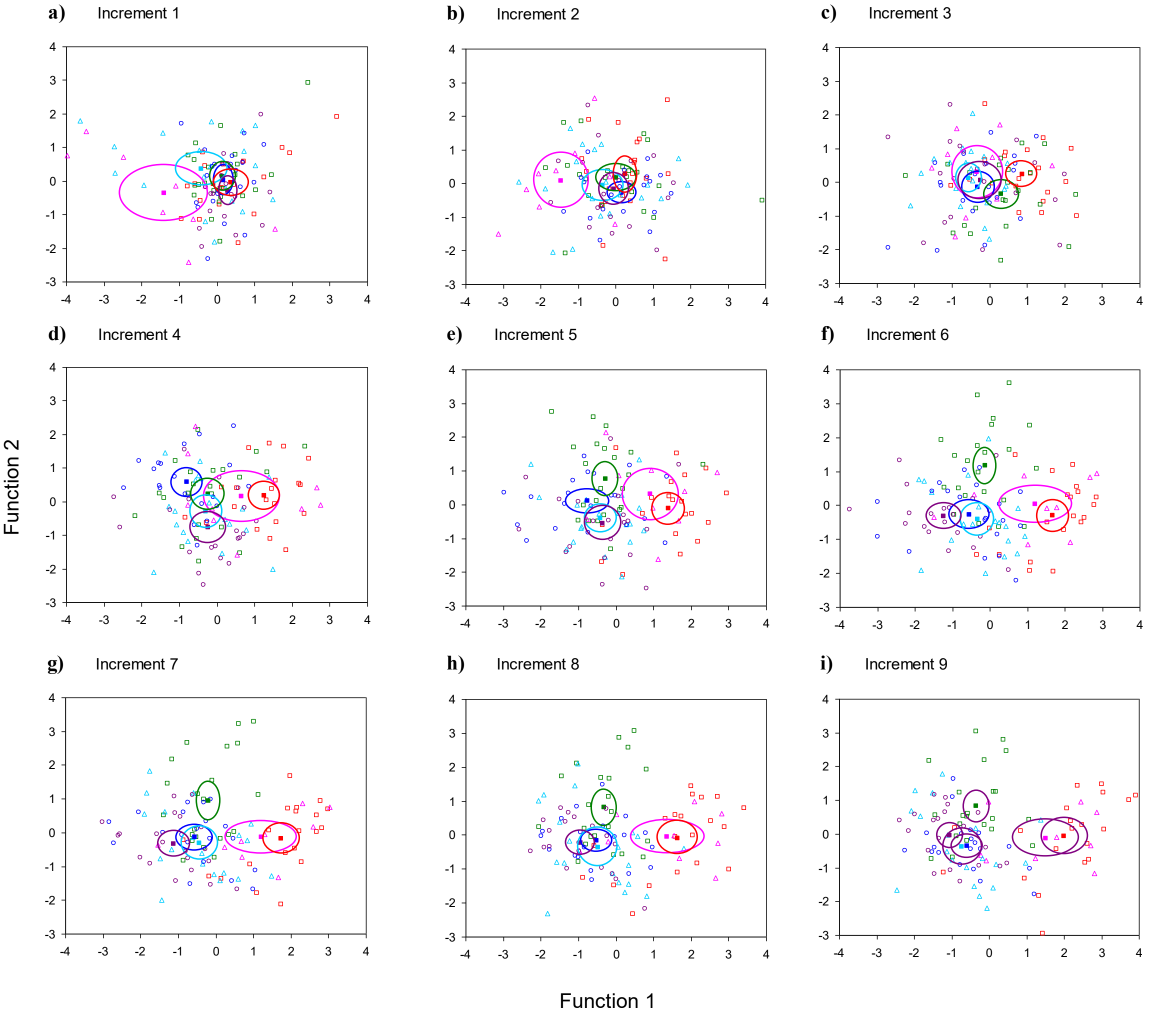

Fig. A10.2. Canonical variate plots for each of the datasets for each of the nine increments analysed as separate datasets. □ = NSG, □ = SSG, △ = NGSV, △ = SGSV, ○ = WC and ○ = SE, solid squares indicate the centroid for each region, and ellipses represent the 95% confidence intervals about the centroid.

Within-region variation in age-related profiles

There were clearly age-related differences amongst regions in the characteristics of the otoliths. However, there was also considerable variation amongst the individual elemental profiles that were summarised in the average estimates provided in Fig. A10.1. This is important to recognise since it suggests there were likely some differences in the pathways that were taken by individual fish throughout their lives to end up in the places where they were ultimately captured. Such variation is evident in the average age-related means for the different fish (Fig. A10.3), as well as the profiles of elemental concentrations across the individual otoliths (presented in Appendix in Fowler et al. 2004). This within-region variation is demonstrated in the following descriptions of the profiles of age-related profiles for ^{138}Ba (Fig. A10.3).

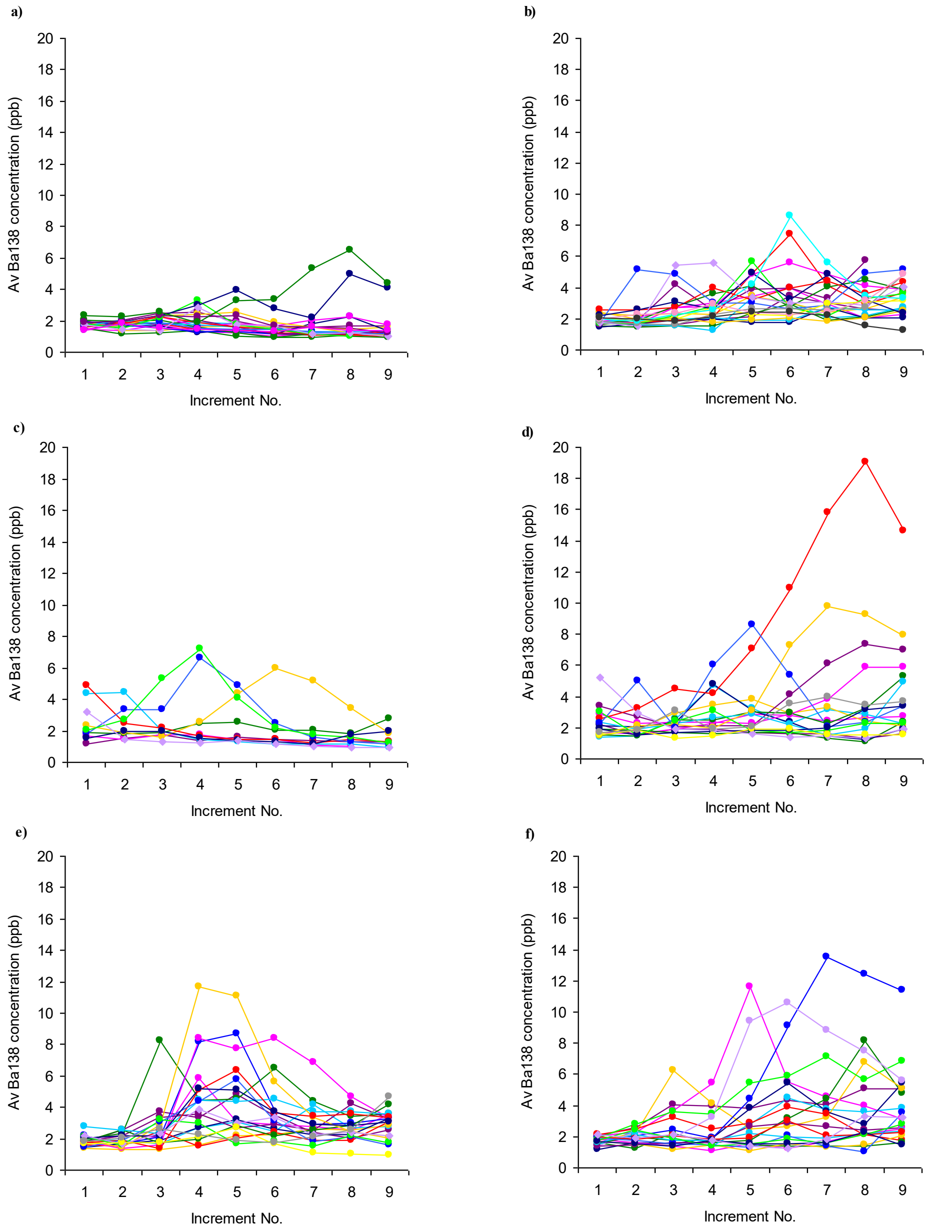

Fig. A10.3. Profiles of average barium concentration for increments from the core to outer edge for each fish from each region; a) – NSG, b) – SSG, c) – NGSV, d) – SGSV, e) – WC, f) – SE.

For NSG, the barium concentrations were characteristically low, i.e., generally <3 ppm, and showed little age-related variation (Fig. A10.3a). Only for two fish, did an age-related mean exceed the concentration of 5 ppm. For the fish from SSG, the barium concentrations were perceptibly higher and more variable than for NSG (Fig. A10.3b). For the first increment or two, the Ba concentrations were relatively low, similar to those for NSG. Generally, for the third increment, higher levels of barium were recorded, which remained evident across the otoliths. There were numerous otoliths that had peaks in some years in Ba concentrations of 5 – 10 ppm. The ages at which these peaks occurred varied amongst individuals. For WC, the age-related barium profiles were generally characterised by high intra- and inter-annual variability. Nevertheless, the first few annuli had low levels of Ba, similar to those from NSG (Fig. A10.3e). From the 3rd or 4th increment onwards, the Ba levels and their variability increased. For the latter increments, the Ba levels declined.

Despite the small sample size for Snapper considered from NGSV, there were several types of profiles of Ba concentrations evident. Several displayed the invariant profiles that were typical of NSG for which the concentrations remained below 5 ppm (Fig. A10.3c). Several otoliths displayed elevated levels of Ba of 5 – 10 ppm during either their 3rd, 4th or 5th years. These remained elevated for a year or two before declining to a low level. The third type of profile showed an elevated level of Ba primarily in the first year, which for one fish extended into a second year. They subsequently had low Ba concentrations. For the SGSV fish, several Ba Profiles were evident. Most otoliths had low levels of Ba for the first few increments after which the Ba levels increased (Fig. A10.3d). There were also several otoliths for which the Ba levels were notably invariant and low, before increasing in the most recent year or two. There were several otoliths which showed high levels of Ba in the first annual increment, which then declined to lower levels in subsequent years.

For the SE Region, the Ba profiles initially showed low Ba concentrations for the first few years, similar to those from NSG (Fig. A10.3f). For several otoliths, the profiles increased over time and remained relatively high. Alternatively, there were some that had low levels of Ba consistently across the otoliths.

Summary of within-region and inter-regional comparisons

The inter-regional comparison of the age-related mean values of IncW, Av88SR and Av138Ba clearly identified that for the first three increments the otoliths were uniform in their characteristics. In comparison however, for the remaining 4th to 9th increments, there were significant regional differences in both increment widths and elemental concentrations. These regional differences should not be interpreted to suggest that at the within-region spatial scale the otoliths were uniform. The data for individual fish at this scale demonstrated considerable variation both amongst age classes within individual otoliths and between otoliths. These suggest the likelihood of different natal origins and different inter-regional movement patterns that culminated in the fish being captured as nine-year olds in the different regions.

10.6.2 Regional comparisons for the 1991, 1997, 2001 and 2004-year classes

The second otolith chemistry study for Snapper in South Australia was undertaken between 2012 and 2014, as part of FRDC Project 2012/020 (Fowler 2016, Fowler et al. 2017). It considerably increased the scope of the previous study. First, the otoliths from four different year classes were considered, which had been recognised from age structures as strong year classes for some regional populations (Appendices Chapter 9). Furthermore, the study also considered otoliths from Port Phillip Bay (PPB), Victoria, the primary nursery area for the Western Victorian Stock (Hamer et al. 2006, 2011).

The methods were similar to those in the previous study. Transverse sections were prepared of otoliths from the 1991, 1997, 2001 and 2004-year classes that had been sampled from several regions (NSG, SSG, NGSV, SGSV, SE and PPB). The concentrations for several elements were then sampled across the chronological structure of these otoliths using laser ablation ICPMS. The resulting profiles were used to calculate age-related estimates of concentrations of Ba:Ca, Sr:Ca, Mn:Ca and Mg:Ca, which were then compared amongst regions. For the fish collected from different regions, the significant regional differences in elemental concentrations were used to infer the natal origins and patterns of inter-regional movement.

1991 Year Class

A total of 79 otoliths were considered from the 1991-year class from five regions, i.e., NSG, SSG, NGSV, SGSV and PPB. The otoliths from the South Australian regions were collected from fish captured in 2003, whilst those from PPB had been collected in 2000.

The elemental profiles in otoliths from PPB clearly differed from those of the South Australian regions (Fig. A10.4). Across all age-classes, the otoliths from PPB had the highest concentrations of Ba:Ca and Mn:Ca, high Mg:Ca ratios for some age classes, but low concentrations of Sr:Ca. These resulted in significant multivariate differences in the otolith chemistry between PPB and the South Australian regions (Fig. A10.4). The considerable extent of these differences tended to dwarf the differences amongst otoliths from the South Australian regions. The only significant age-based differences amongst the latter were for the 4-5 and 5-6 increments, which likely related to differences in Sr:Ca concentrations.

1997 Year Class

A total of 78 otoliths were considered for the 1997-year class that were from the same regions as considered in 1991. The South Australian fish were sampled at 11+ years of age and were collected in 2008, whilst the otoliths from the PPB fish were 7+ fish having been collected in 2004.

The biggest differences in otolith chemistry were between those from PPB and the South Australian Regions (Fig. A10.5). The former had the highest estimates of Ba:Ca and Mn:Ca for most increments. These resulted in significant multivariate regional separation between those from PPB and the otoliths from all South Australian regions (Fig. A10.5). There were also some notable differences amongst the latter, for which separation between the otoliths from NGSV and those from NSG and SSG appear to relate to age-related estimates for Ba:Ca and Sr:Ca.

2001 Year Class

For the 2001-year class, 91 otoliths were considered from five regions in South Australia and from PPB, Victoria. They were all in the 8+ age class and were sampled in 2009.

There were significant age-related differences amongst regions for each of Ba:Ca, Sr:Ca, Mn:Ca and Mg:Ca (Fig. A10.6). These differences were particularly evident for Ba:Ca. For NSG, SSG and NGSV, the Ba:Ca ratios were generally low in contrast to those from PPB, SE and SGSV for which the average annual Ba:Ca ratios were generally considerably higher. The multivariate analyses indicated significant inter-regional differences in otolith chemistry (Fig. A10.6). For each increment, these primarily related to differences between two groups, i.e., PPB, SE and SGSV, and a second group that involved NSG, SSG and NGSV. SSG least conformed to this division, as at increments 3-4 and 4-5, the otolith chemistry diverged from that of the northern gulfs and became more similar to that of the three southern regions of PPB, SE and SGSV.

2004 Year Class

For this year class, there were 91 otoliths considered that were collected in 2009 from the 5+ age class. They were from the five South Australian regions as well as from PPB.

The estimates of Ba:Ca, Sr:Ca and Mn:Ca for the first few increments were divisible into two groups. The otoliths from PPB and the SE had high levels of Ba:Ca, Sr:Ca and Mn:Ca, compared with those from the four regions in the SA gulfs (Fig. A10.7). For the later formed increments, differences emerged amongst the SA gulf regions. Gradually, the multi-elemental signal of otoliths from SGSV diverged from that of the northern gulfs, whilst that from SSG gradually diverged from that of NSG.

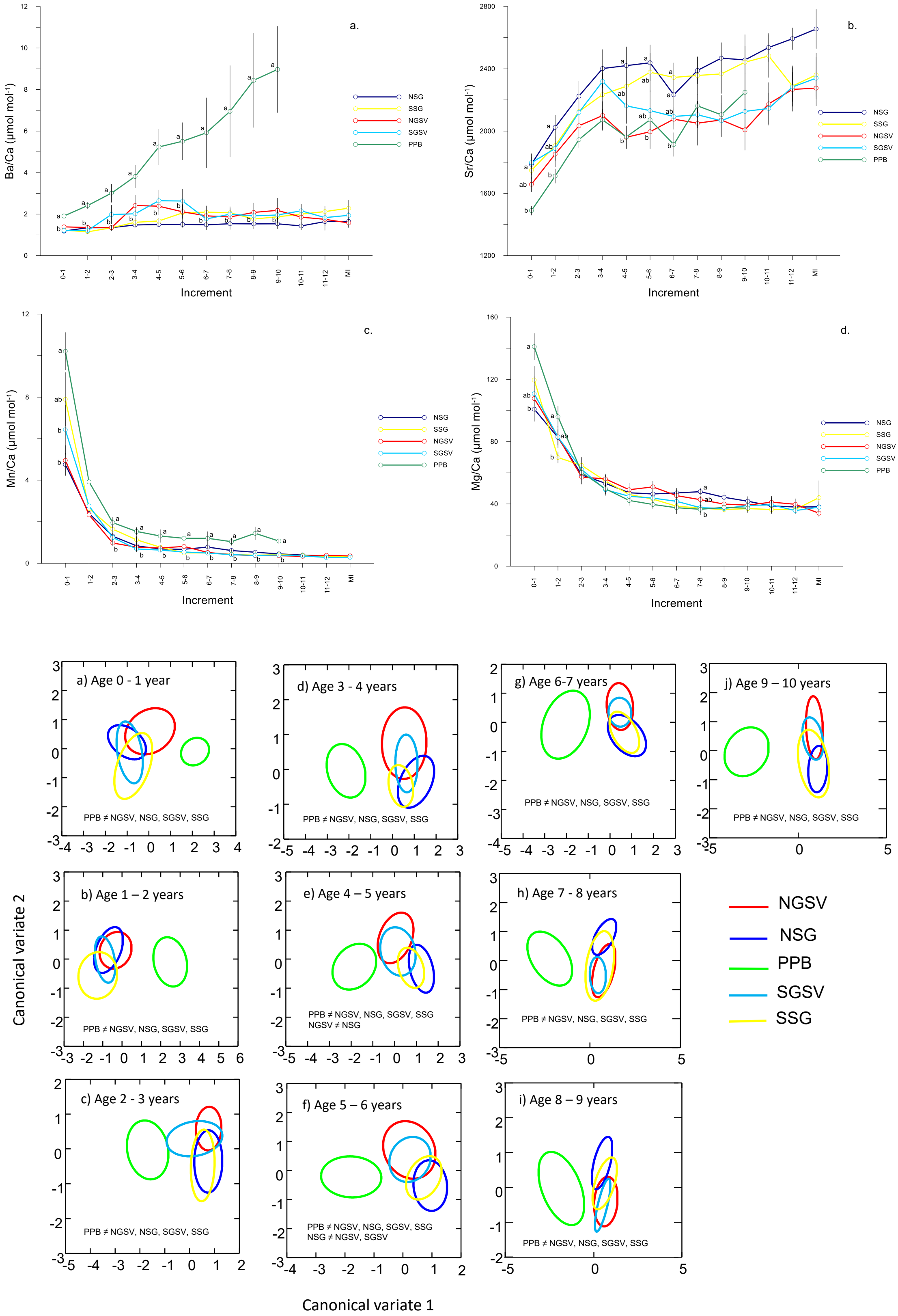

Fig. A10.4. Top - regional comparisons of age-related element:Ca ratios across otoliths of Snapper from the 1991-year class for a. Ba:Ca, b. Sr:Ca, c. Mn:Ca and d. Mg:Ca. Bottom – canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the 10 annual increments considered for the 1991-year class. Data shown are the 95% confidence ellipses around the regional means. Results of pairwise tests subsequent to the MANOVAs are provided as text in each plot.

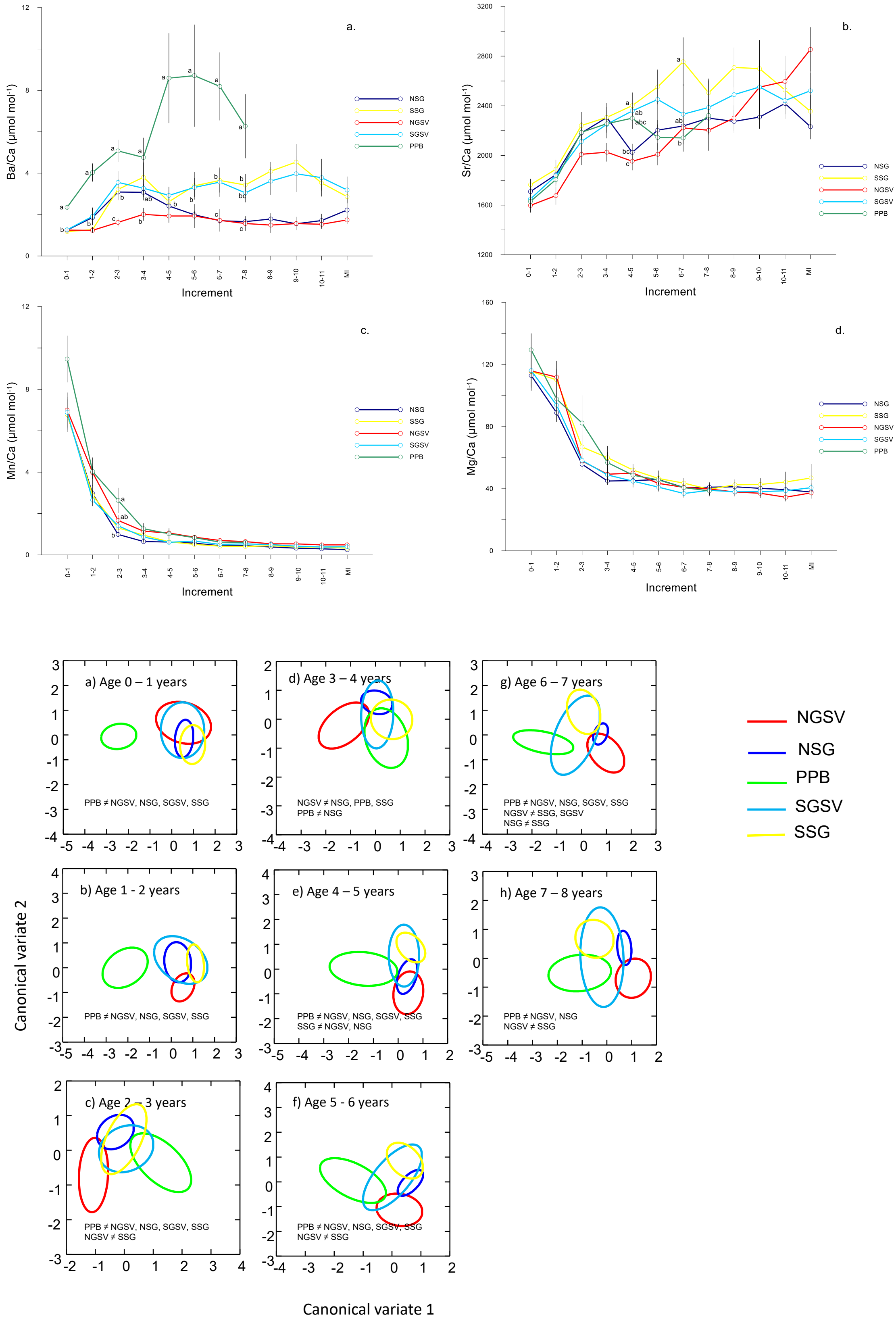

Fig. A10.5. Top - regional comparisons of age-related element:Ca ratios across otoliths of Snapper from the 1997-year class for a. Ba:Ca, b. Sr:Ca, c. Mn:Ca and d. Mg:Ca. Bottom – canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the eight annual increments considered for the 1997-year class. Data shown are the 95% confidence ellipses around the regional means. Results of pairwise tests subsequent to the MANOVAs are provided as text in each plot.

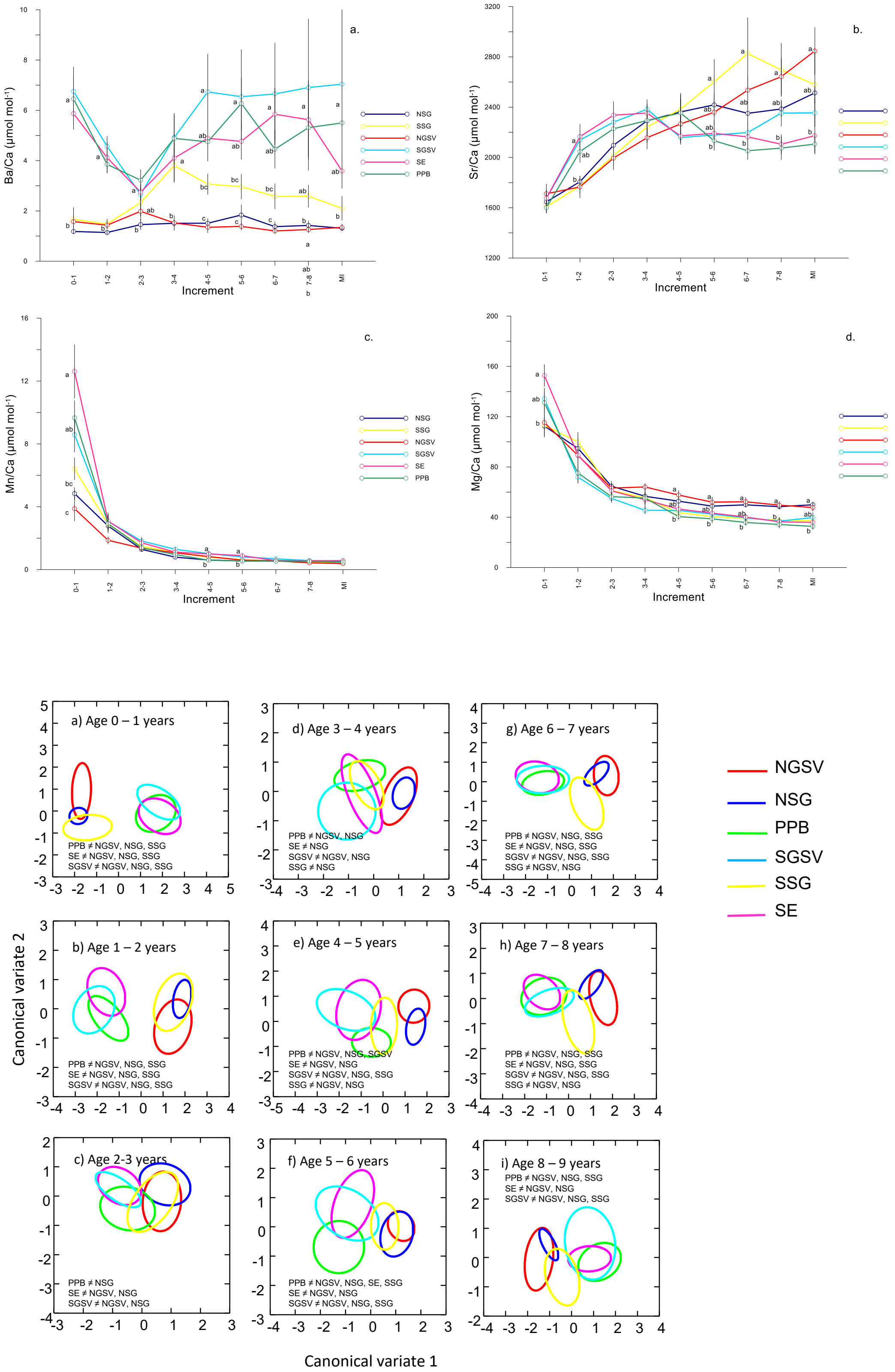

Fig. A10.6. Top - regional comparisons of age-related element:Ca ratios across otoliths of Snapper from the 2001-year class for a. Ba:Ca, b. Sr:Ca, c. Mn:Ca and d. Mg:Ca. Bottom – canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the nine annual increments considered for the 2001-year class. Data shown are the 95% confidence ellipses around the regional means. Results of pairwise tests subsequent to the MANOVAs are provided as text in each plot.

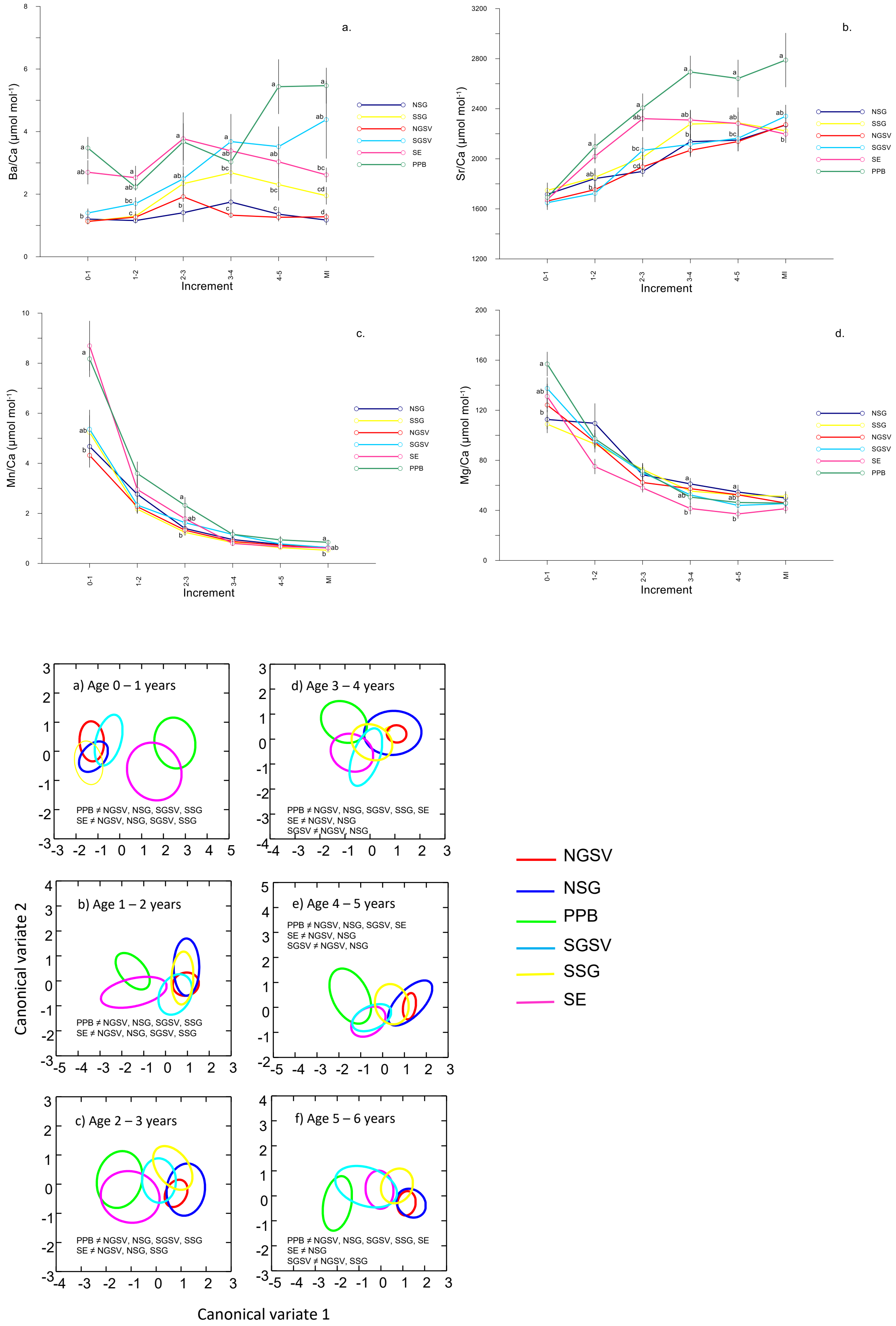

Fig. A10.7. Top - regional comparisons of age-related element:Ca ratios across otoliths of Snapper from the 2004-year class for a. Ba:Ca, b. Sr:Ca, c. Mn:Ca and d. Mg:Ca. Bottom – canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the six annual increments considered for the 2004-year class. Data shown are the 95% confidence ellipses around the regional means. Results of pairwise tests subsequent to the MANOVAs are provided as text in each plot.

11. ACOUSTIC TELEMETRY – MOVEMENT AND BEHAVIOUR

Anthony Fowler, Charlie Huveneers, Matthew Lloyd

11.1 Introduction

The dispersion of the individuals of an animal species in space and time relates to the habitat configuration of their environment including the presence or absence of conspecifics (Brown and Orians 1970). Implicit to the dispersion of individuals is their movement behaviour, i.e., the distances they move and places they visit to access food and shelter, the relative availability of these resources and the inter- and intra-specific interactions that occur in accessing them (Andrewartha and Birch 1954). For a species whose population biology is of interest, it is important to understand such environmentally-driven spatial dispersion because it influences the dynamics and densities of populations, as well as genetics and species evolution (Brown and Orians 1970). Furthermore, animal movement and the dispersion of individuals contribute to ecosystem structure and functionality. This can have practical significance for the spatial management of fisheries and for conservation purposes. For example, for marine reserves to be ecologically useful they must be of a size and habitat configuration commensurate with the mobility and resource requirements of significant species (Baker 2000, Parsons et al. 2003).

Across its broad distribution in Australasia, Snapper (*Chrysophrys auratus*) is an important fish species from ecological and fishery perspectives that inhabits a broad depth range and diversity of habitats from coastal bays and inlets to offshore on the continental shelf (Kailola et al. 1993). Studies of Snapper movement have been undertaken since the 1960s. The earlier studies used tag/recapture techniques (Paul, 1967, Sanders 1974, Crossland 1976, Jones 1981, 1984, Moran et al. 2003, Sumpton et al. 2003, McGlennon 2003, Norriss et al. 2012), whilst recent ones have generally been based on otolith chemistry analysis (Fowler et al. 2005, Hamer et al. 2005, 2006, 2011) or acoustic telemetry (Hartill et al. 2003, Parsons et al. 2003, 2010, Egli and Babcock 2004, Harasti et al. 2015, Fowler et al. 2017). The numerous tag/recapture studies demonstrated that at different places Snapper showed specialised, idiosyncratic migratory patterns (Moran et al. 2003). Most studies consistently demonstrated that whilst some Snapper moved distances of 100s of km, most recaptures of tagged fish were made within only a few km of the initial tag site. McGlennon (2003) differentiated this range of movement behaviours into 'residents' and 'migrants'. A general conclusion from the tagging studies was that most Snapper did not move far relative to their capabilities for movement. This has been supported by findings from several local studies undertaken in New Zealand that showed that Snapper have strong site fidelity, restricted ranges of movement and occupy limited home ranges within which their activity is concentrated in just one or two local areas (Kingett and Choat 1981, Willis et al. 2001, Parsons et al. 2003, Egli and Babcock

2004, Parsons et al. 2010). Until recently, such local studies were rare for Australian populations of Snapper (but see Harasti et al. 2015), which meant that for such populations, there was a better understanding of large-scale movement over distances of 100s of km than there was for local movement over distances of only metres to kms.

The purpose of this chapter was to summarise several studies that were undertaken in South Australia during the 2000s to investigate local and within-region movement behaviour of Snapper to contribute to development of appropriate management strategies. The methodology used for these movement studies was acoustic telemetry. This involves the complementary use of acoustic transmitter tags that were implanted in sub-adult and adult Snapper and the use of in situ acoustic receivers that record detections from the acoustic tags. The latter provide presence data through time at specific locations, the time series of which can be interpreted as fish behaviour in terms of movement, site fidelity and periods of occupancy (Heupel et al. 2006, Heupel and Webber 2012). Three such studies have been done for Snapper in South Australia. The first was done in northern Spencer Gulf in 2009/10, the second in northern Gulf St. Vincent from May 2011 to July 2014, and the third was also done in Gulf St. Vincent between November 2020 and February 2021. Here, the focus is on the first two studies, providing details on their context, objectives, where they were done, their duration, methods, and summaries of results. Whilst the second study has previously been described in detail (Fowler 2016, Fowler et al. 2017), the first study had not yet been described.

11.1.2 Northern Spencer Gulf

In 2009, concern was emerging about the status of the Snapper fisheries in Northern and Southern Spencer Gulf. At that time, commercial catches and catch rates were declining, reflecting the consequence of relatively poor recruitment to Northern Spencer Gulf (NSG) since 1999 (Fowler et al. 2010). Our understanding of the reproductive behaviour of the adult fish during the summer spawning aggregations and the significance of egg production to variable recruitment was poor. This study was undertaken to describe the local behaviour of adult Snapper at and between two adjacent aggregation sites. At that time, the fishery management regime involved a seasonal fishery closure during the month of November (Fowler et al. 2020). There was interest in the impact of the closure and the behaviour of the fish when the fishery was reopened each year at midday on the 30th November. The specific objectives addressed in this study were:

1. to describe the movement behaviour and residence of Snapper at different temporal scales at two adjacent aggregation sites located 5nm apart;
2. to determine the level of connectivity between these sites;
3. and to assess the behaviour of the fish at the re-opening of the fishery on the 30th November.

11.1.3 Northern Gulf St. Vincent

The second study on the movement behaviour of Snapper in South Australia that used acoustic telemetry was done between 2011 and 2014 in Northern Gulf St. Vincent. At that time, this region was producing near record commercial catches (Fowler et al. 2010, 2013). The management focus was to ensure the long-term sustainability of the fishery in the face of the declining fishery in Spencer Gulf. This, however, was challenging because of the limited understanding about the processes that led to the regional increase in biomass and the behaviour of Snapper throughout the region with respect to their movement, residence, and habitat and resource use. This study addressed the latter shortcoming by investigating local and within-region movement behaviour of Snapper to provide understanding about behaviour that would inform developing management strategies. The specific null model that was considered was based on earlier acoustic telemetry studies done in New Zealand, where individual Snapper typically exhibited strong site fidelity and had long periods of occupancy of restricted home ranges that had centres of activity that were of limited size (Hartill et al. 2003, Parsons et al. 2003, 2010, Egli and Babcock 2004). The specific objectives addressed were:

1. to describe behaviour at seasonal and annual temporal scales
    a. in terms of the locations and habitats occupied
    b. distances moved, and their timing and locations;
2. to interpret movement in terms of the stock structure and contribute to determining the appropriate spatial scale for managing South Australia’s Snapper fishery.

11.2 Materials and methods

11.2.1 Northern Spencer Gulf

This study was done at two sites in NSG. The first was the shipwreck of the *Illusion* (33°48’S, 137°54’E), a trawler that sank on the 1st December 1981 (Fig. 11.1). This has been a significant aggregation site for Snapper that has attracted considerable fishing pressure from the commercial and recreational fishing sectors. At least since 2000, it has been an important spawning site, determined from our sampling of adult Snapper (Chapter 2). The wreck is located in the middle of the gulf northwest of Port Broughton at approximately 16 m depth. The second site was the Plank Shoal Light, located approximately 5 nm to the west of the *Illusion*. Large Snapper were known to visit this site regularly during the spawning season.

On the 9th November 2009, six Vemco VR2W acoustic receivers were deployed around the *Illusion* as a rectangular array that was oriented from northeast to southwest (Appendix Table A11.1). On the following day, four similar receivers were deployed as a square array around Plank Shoal Light. Each detector was attached to a mooring that consisted of a concrete-filled car tyre with embedded and protruding chain (Fig. 11.2). The acoustic receiver and an automatic acoustic release were shackled to the chain. A large buoy was attached to the top of the arrangement, which kept the acoustic receiver floating above the seabed when the system was in place. On the 10-11th November 2009, 13 Snapper were captured on rod and line, tagged with Vemco V9 acoustic transmitter tags and then released at the capture locations (Table A11.2). Eight fish were tagged in the vicinity of Plank Shoal Light and five at the *Illusion*. The tagged fish ranged in size from 31 to 76 cm CFL.

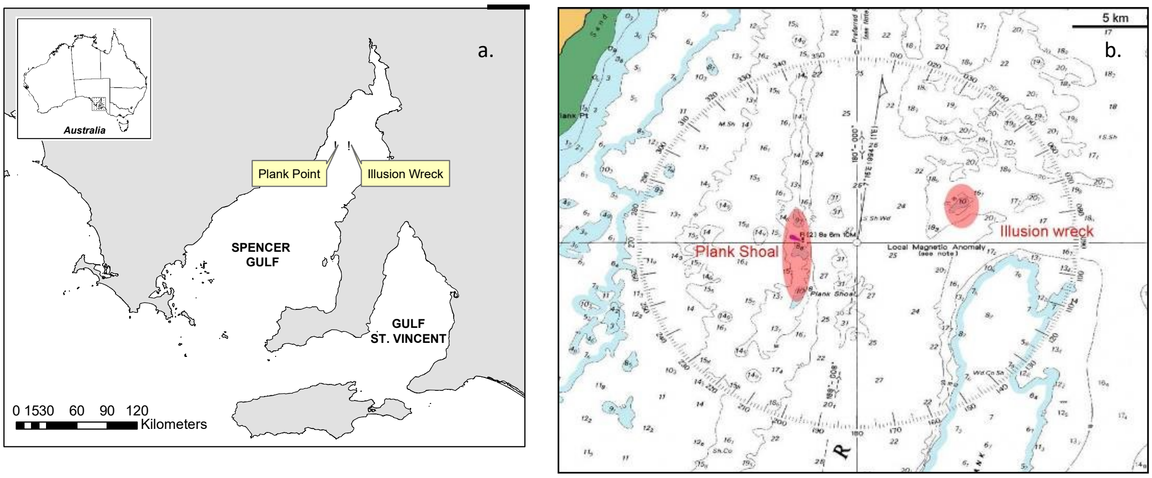

Fig. 11.1. Maps showing the location of the acoustic telemetry study done in Northern Spencer Gulf in 2009-10. a. Large-scale map showing the location of the study area in Northern Spencer Gulf. b. Chart showing the relative locations of Plank Shoal and the wreck of the *Illusion*.

Each fish was caught with rod and line, brought aboard using a small sling and then anesthetised using AQUI-S at a concentration of 1.5 ml in a 50 L seawater bath (30 ppm). The anaesthesia was maintained by recirculating the AQUI-S solution across the fish's gills using a small bilge pump. The fish's eyes were covered with a towel to prevent damage and to reduce stress associated with capture and handling. A small incision (1.5–2 cm) was made lateral to the ventral mid-line anterior to the vent. A Vemco V9-2L coded transmitter (60–180 seconds interval period) was inserted into the body cavity and then the incision was stitched using internal and external sutures (Fig. 11.2). Baytril©50, at a dose of 0.1ml/kg body weight, was injected with a syringe (21 gauge) into the dorsal musculature. The incision was sutured, the fish was recovered from the anaesthetic and then released at the capture location. Generally, the fish were released within 45-50 minutes of capture.

The acoustic receivers were left in situ from the 9th or 10th November 2009 until 10th April 2010, when they were recovered one-by-one from the MRV *Ngerin*. For the recovery of each receiver, the acoustic release was activated, after which the buoy floated to the surface with the acoustic receiver attached. All 10 receivers were successfully recovered. Data on detections of tagged fish were downloaded from the receivers and the data were processed using Excel.

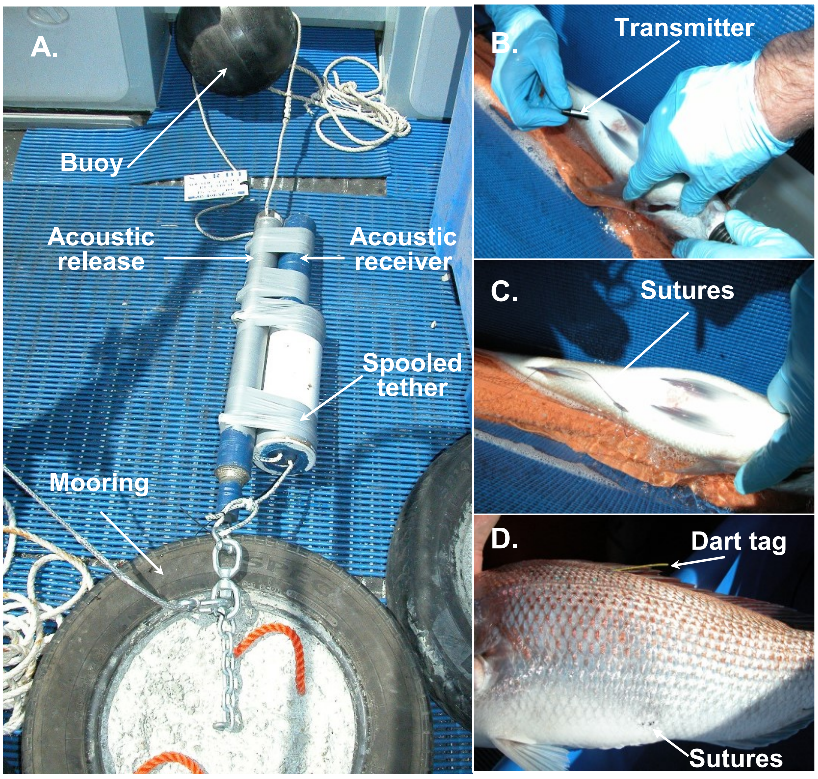

Fig. 11.2. Photographs showing the processes involved in setting up the acoustic telemetry study in Northern Spencer Gulf. A. arrangement of mooring, acoustic receiver, acoustic release and buoy prior to deployment. B. insertion of the transmitter into the coelomic cavity of the fish; C. location of sutured incision near the posterior, ventral area of the fish; D. lateral view of the sutures in situ.

11.2.2 Northern Gulf St. Vincent

The second acoustic telemetry study was done in the northern part of Gulf St. Vincent (NGSV), a triangular-shaped region that narrows towards its apex (Fig. 11.3a). The study was run for approximately three years from late May 2011 until July 2014. Over several days from 17th May 2011, an array of VR2W Vemco acoustic receivers was established throughout the study area, augmenting several lines of receivers that had previously been deployed along the eastern coastline of Gulf St. Vincent to monitor the movement of whaler sharks (*Carcharinus* spp.) (Fig. 11.3a). The study area in NGSV consisted of six contiguous smaller component areas (AN, AR, AG, ZN, BP and LS) (Fig. 11.3b). The receivers were deployed in or near several different types of benthic habitats that included small natural and artificial reefs, mussel beds, beds of razor fish (*Pinna dolabrata*) and seagrass meadows. One station, i.e., 17ZN, was positioned next to the largely intact shipwreck of the '*Zanoni*', a three-masted sailing vessel of 42.4 metres in length that sank in 1865. Whilst its bow, stern post and rudder once stood nearly six metres above the seafloor, the wreck has degraded is now likely only 2 m high. Historically, this large structure attracted considerable fishing effort from the commercial and recreational sectors. So, to protect it, in 1984, a barge of 39.9 m in length was sunk one nautical mile south of the *Zanoni*, to provide an alternative place for fishing.

From year to year, the acoustic array was modified with respect to the number of receivers and their configuration (Appendix Table A11.3). In April 2012, during the first data retrieval, the modifications to the configuration of the array for the second detection period until May 2013 included the addition of six receivers, the removal of several stations, whilst one receiver that was lost was not replaced (Appendix Table A11.3, Fig. 11.2b). In July 2013, a further 10 receivers were deployed in area 'AR'. Across the three years, 18 stations were maintained, 13 were maintained for two years, whilst 10 stations were established for only the last year of the study. The number of receivers deployed throughout the gulf ranged from 50 to 67 (Table 11.1).

Table 11.1. Number of acoustic receivers deployed during each year in each component area of the study area, total number for the study area in NGSV and total for GSV. For configuration of array in each year refer to Fig. 11.2.

Detection period	Area						NGSV –	GSV –
	BP	AN	AR	AG	ZN	LS	total	total
May 2011 – April 2012	2	2	8	1	2	10	25	50
April 2012 – May 2013	0	3	10	3	2	13	31	57
May 2013 – May 2014	0	3	20	3	2	13	41	67

All acoustic receivers were deployed attached to star pickets. Each receiver was positioned vertically 0.5-1 m above the seabed, with the hydrophone located above the star picket. Some were deployed by scuba divers whilst for others the picket was embedded in a concrete mooring which was then lowered to the seabed.

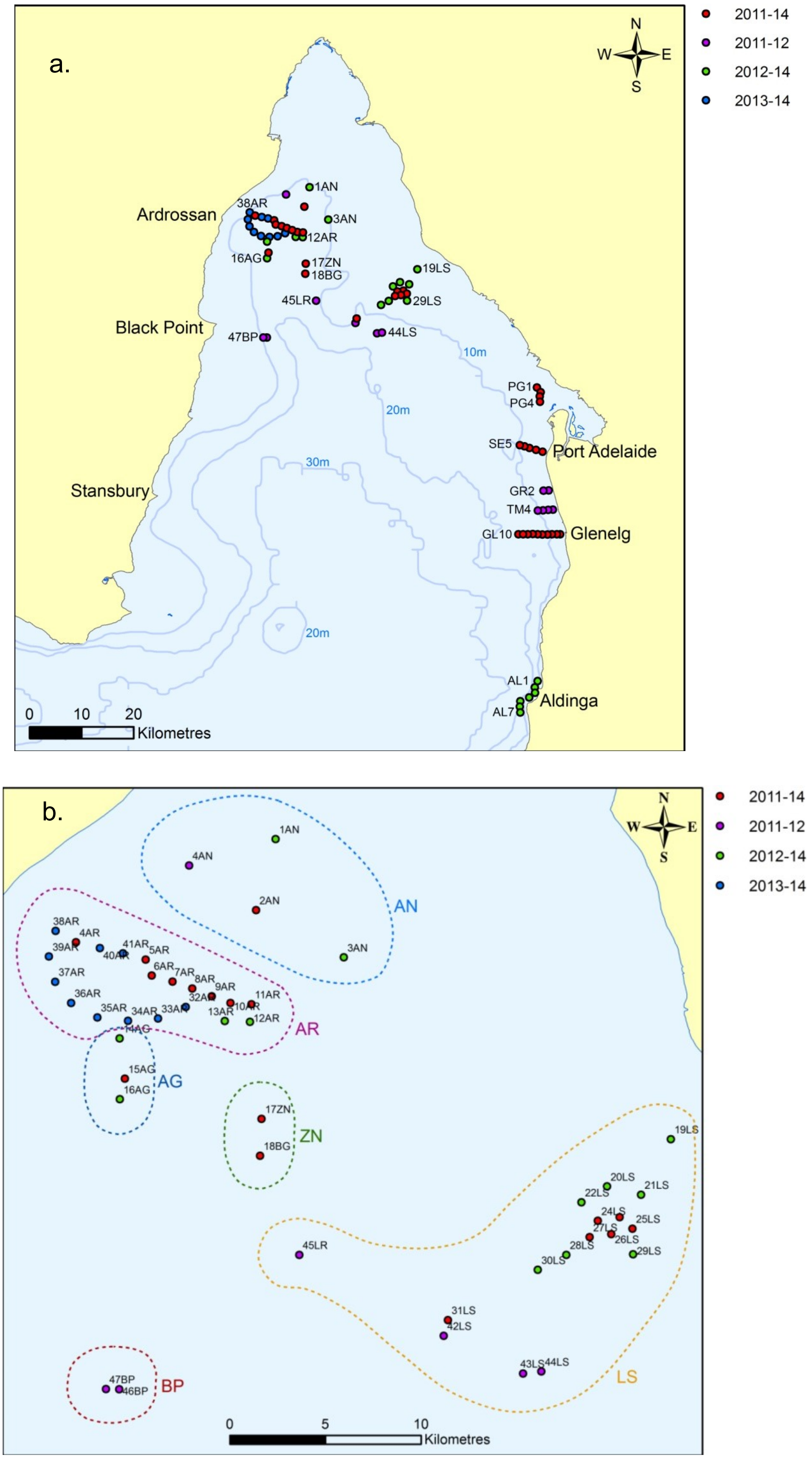

Fig. 11.3. Maps showing the configuration of acoustic receivers deployed throughout the three years of the acoustic telemetry study for Snapper. a. Map of Gulf St. Vincent showing the array of receivers in the northern gulf and lines of receivers along the metropolitan coastline. Depth contours are indicated. b. Map of study area in Northern Gulf St. Vincent showing the distribution of acoustic receivers throughout the six component areas in each year. Dotted lines are illustrative only and do not represent specific borders.

11.2.3 Acoustic tagging

Between 26 May 2011 and 23 May 2014, 54 Snapper were successfully tagged with acoustic transmitters and released (Appendix Table A11.4). Fish were captured using handlines or longlines, some within the vicinity and some further away from the array (Fig. 11.4). For details of capture and tagging techniques and types of acoustic tags that varied in physical dimensions according to battery type, power level, and presence/absence of a pressure sensor for recording water depth, refer to Fowler et al. (2016, 2017). The 54 tagged fish covered the broad size range of 32 to 97 cm caudal fork length (CFL). Most ‘small’ (<40 cm CFL) and ‘medium’ fish (40-60 cm CFL) were captured with rod and line and were tagged with V13 tags. The ‘large’ >60 cm CFL and ‘very large’ (>80 cm CFL) fish were captured with longlines and tagged either with V13P or V16 tags.

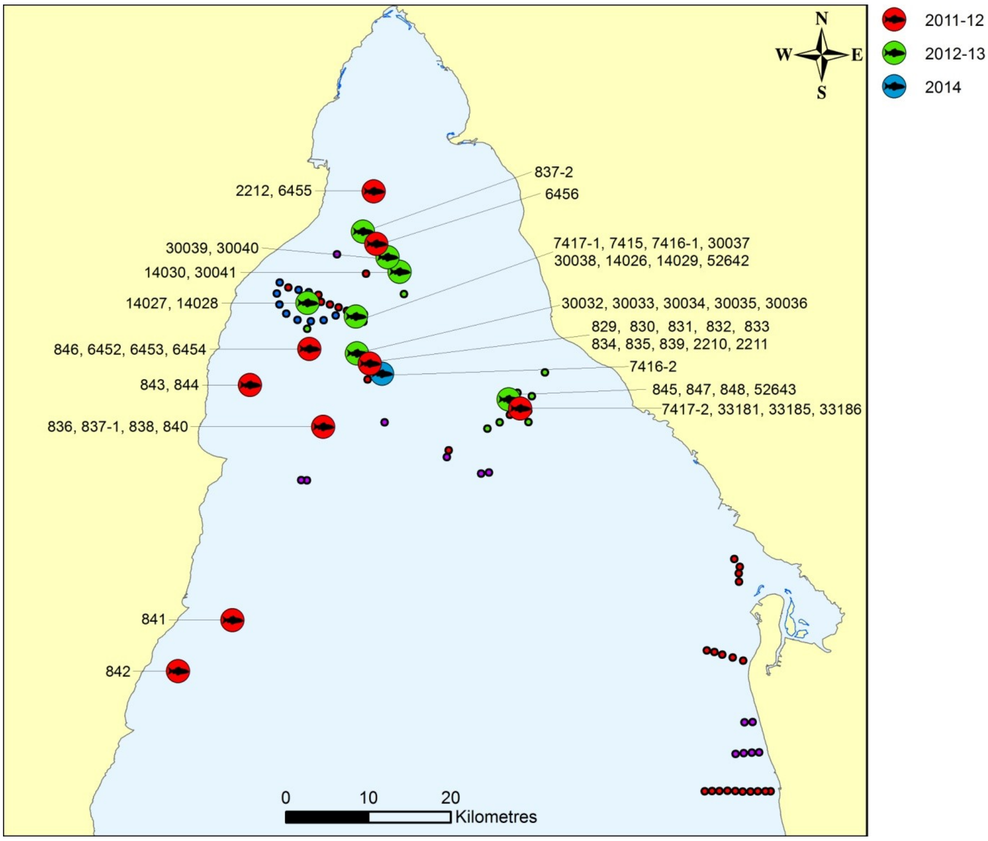

Fig. 11.4. Map of Gulf St. Vincent showing the places where Snapper were captured, tagged with acoustic tags and then released. Numbers indicate the identification number of each fish (Table A11.4). The locations of acoustic receivers are also shown.

11.2.4 Analysis of habitat

Previous surveys have provided some information about the benthic environment in Gulf St. Vincent (Shepherd and Sprigg 1976, Tanner 2005). The gulf provides a relatively low energy environment that is slowly being filled in by sediment deposition (Tanner 2005). As such, most of the benthic substrate is either sand or fine silt, with few areas of hard bottom. The original survey identified that the northern region had two dominant benthic habitats; the coastal margins supported seagrass meadows that predominantly involved *Posidonia* spp., whilst the deeper waters offshore between Black Point and Ardrossan were dominated by a Pinna-Holothurian assemblage (Shepherd and Sprigg 1976). The second survey noted considerable habitat changes in Gulf St. Vincent, but these were predominantly in the southern and central areas (Tanner 2005). The northern region appeared to have experienced less degradation compared to the southern part of the gulf, possibly due to low terrestrial run-off and the low level of prawn-trawling done in this region.

Benthic habitat mapping was undertaken as part of this study. At 142 stations in the vicinity of the study area in NGSV, the benthic habitat was sampled either with video imaging or by direct observation by scuba divers (Fig. 11.5). In December 2012, at each station, a video camera was deployed to within 0.5 to 1 m of the seabed and video footage of the benthic substratum was recorded for approximately 100 m. Later, when this footage was processed the sediment type, the dominant taxa of flora and fauna were identified, and a general habitat classification was assigned for each station. The substratum was classified as either silt or silt/sand by percentage cover, whilst the primary categories of habitat were: razorfish on bare substratum; razorfish with mixed algae/seagrass; razorfish with *Posidonia* spp.; seagrass meadows with either *Posidonia* and/or *Amphibolis* spp.; Ascidian dominated assemblage.

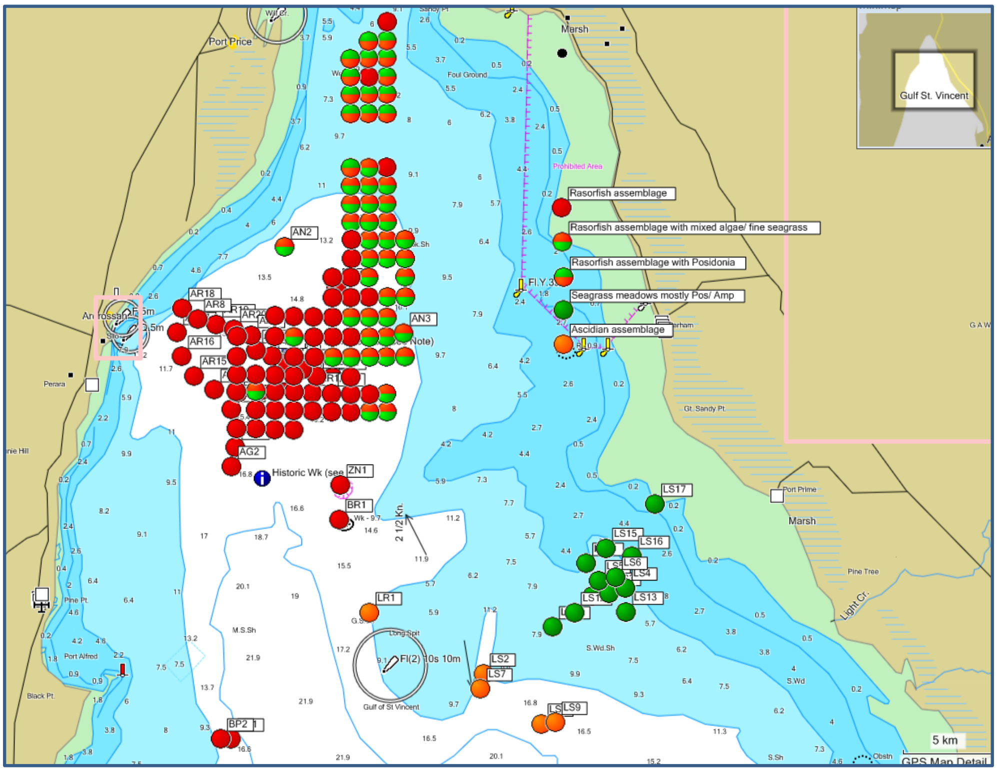

Fig. 11.5. Map of Northern Gulf St. Vincent showing the general habitat classifications that were assigned to the numerous stations where benthic habitat mapping was done.

This benthic analysis indicated that the two major habitat types persisted in NGSV, although with some areal variation. The deeper waters of the AN, AR, AG and ZN areas throughout which the acoustic receivers were distributed, were dominated by flat substratum throughout which were distributed razorfish, whose densities generally ranged from sparse to moderate (Fig. 11.5). Further to the east, the razorfish were scattered amongst seagrass and/or algae and to the north they were distributed throughout the *Posidonia* beds. The LS area was dominated by sand or silt bottom that supported meadows of *Posidonia* or *Amphibolis* spp. In the western part of the LS area, there were several stations that supported sparse Ascidians.

11.2.4 Data retrieval and analysis

Space use – timing and duration of occupancy of study area

The acoustic receivers were retrieved by scuba divers and downloaded on three occasions: 16-19 April 2012; 17-19 May 2013; and at the end of the sampling program from 20-23 May to 22 July 2014. The data on detections from the acoustic tags were processed using Excel, with pivot tables used to generate totals of detections at the spatial scales of amongst stations and amongst areas. The detection data were also used to describe the use of the study area at several temporal scales. The temporal analyses were complicated because there were significant environmental influences on the acuity of the system to record detections at daily and seasonal temporal scales (Huveneers et al. 2012, Fowler et al. 2016, 2017). The results from two long-term sentinel tags informed about these influences. They provided quantitative estimates of the acuity of the system that allowed raw numbers of detections to be standardised using standardised detection frequencies (SDFs) (Payne et al. 2010), to provide more accurate estimates of the temporal trends in detections. Such standardisation was done at several temporal and spatial scales (Fowler et al. 2016, 2017).

11.3 Results

11.3.1 Northern Spencer Gulf

Detections were recorded from 10 of the 13 tagged fish (Table A11.2). Of three for which there were no detections, two had been tagged at Plank Shoal and one at the *Illusion*. Only for one of these was there some information about its fate following release. Having been captured and tagged at Plank Shoal, Fish 227 was recaptured on 27th December 2009 by a recreational fisher, indicating that it had survived the tagging process. A further three fish produced relatively low numbers of detections (Table A11.2). At least two of these survived the capture and tagging. For Fish 228, there were 12 detections, mostly recorded between 13:54 and 14:37 hours on the same day as when tagged and released at Plank Shoal. However, there was one further detection for this fish on the 2nd February 2010 that was recorded at the *Illusion*. Fish 229 provided only one detection several hours after it was released at the *Illusion*. It was recaptured at Plank Shoal on the 13th March 2010. Fish 237 produced 23 detections at Plank Shoal immediately after it was tagged and released on 11th November 2009, but it was not detected or recaptured subsequently.

The remaining seven fish produced a total of 9,571 detections that ranged from 194 to 4,008 detections.fish^{-1} (Table A11.2). Most detections were recorded between the release date and the 1st December 2009, after which the rate declined significantly and then ceased during the first week of December (Fig. 11.6). Fish 225 was an exception as relatively high numbers of detections were recorded until early January 2010 with one further detection on 15th February 2010. For Fish 230, there were occasional detections during December and January, whilst for Fish 231 there were a few detections recorded in March 2010.

Plank Shoal

For three fish tagged near the array at Plank Shoal, most detections were recorded during several weeks after the fish were tagged with daily detections recorded until at least the 1st December 2009. Their high numbers of detections accounted for 84.2% of all detections, which were all recorded at Plank Shoal (Fig. 11.7). However, these were not distributed evenly either spatially or temporally. Most detections were recorded on the eastern side of the array at PLE1 and PLE2 (Fig. 11.7). Higher numbers of detections were recorded throughout the day than at night. Also, the daily detection rate.fish^{-1} varied cyclically through November 2009, before declining and remaining low in early December. The timing of the cyclical variation was consistent amongst fish, with high numbers recorded until 13th November, lower numbers for several days before they were high again during the last week of November. The decline in detections to around the 17th November occurred during the waning and new moon, whilst the subsequent increases corresponded to the increasing moon in latter November. Detection rates declined between the 28th and 30th November, and on the 1st December declined considerably and subsequently remained at an incidental level. Between the 11th and 30th November there was no correlation between the detection rates and the wind data for NSG, suggesting that the variation in detection rates was not driven by the weather.

The depths occupied by each fish were recorded as part of the data detections. They varied on several temporal scales, i.e., within and between days, but nevertheless showed some consistencies amongst fish, presumably relating to their behaviour. Between 11th and 16th November, Fish 231 largely occupied the depth range of 5-10 m (Fig. A11.1). Then, from the 17th to 21st November most of the fewer detections were in the 4-6 m range. From 21st to 25th November, the more numerous detections were also concentrated in the 4-6 m depth range, although it was occasionally deeper. The behaviour was different from the 26th to 30th November during which this individual was regularly detected at 2 m depth. Also, there were daily cyclical movements throughout the range of 2 to >8 m depth, with the deeper detections generally recorded during the late afternoon and early evening between 17:00 and 20:00 hours. The relatively few detections from 12:00 on the 30th November onwards were mainly through the range of 2-7 m depth.

For Fish 233, the largest fish considered in this study, its depth regime also varied within and between days (Fig. A11.1). Until the 23rd November, it was largely in the zone of 7 to 12 m. Then, from the 24th to 30th November, it was generally shallower at 5 to 10 m, but with occasional excursions to around 12 m, which generally occurred in the evening between 19:00 and 21:00 hours. The behaviour of Fish 235 was similar to Fish 231 and 233, being consistently shallower from the 24th to 29th November with excursions to >10 m during the evenings of several days.

The *Illusion*

At the *Illusion*, four fish produced moderate detection rates that were approximately an order of magnitude less than those from the array at Plank Shoal (Table Appendix A11.2). Although less clear, the cyclical temporal patterns throughout November were still apparent, whilst detections were generally negligible from 1st December onwards (Figs 11.6, 11.7). The one exception was Fish 225 that continued to produce relatively high numbers of detections throughout December 2009 (Figs. 11.6), most of which were recorded at ILE2 (Fig. 11.7). The other three fish were more commonly recorded at ILW3. Relatively few detections were recorded at ILE3 and ILW2, whilst none were recorded at ILW1 and ILE1, i.e., the detectors located to the northeast of the shipwreck.

The few detections of Fish 224 were recorded in the depth range of 8 to 12 m, although there was one excursion to 14 m on the 28th November at 21:00 (Fig. A11.2). Fish 225 was mainly in the range of 6 to 11 m until the 20th November. Subsequently, it was deeper at 8 to 12 m. Also, there were occasional quick changes in depth from 6 to >12 m that tended to occur during the early evening. Fish 226 was primarily detected throughout the depth range of 6 to 13 m, although shallower for a period on 27th November. Fish 230 was similar until 19th November, after which it was more restricted to 8-12 m.

For no fish were acoustic detections recorded at both Plank Point Light and the *Illusion*. This indicates that regular movement between the sites did not occur during the study. However, there some rare movements between the sites. Fish 224 was tagged and released at Plank Shoal on 10/11/2009 at 12:37, but all detections were recorded at the *Illusion* commencing at 17:19 on the same day (Fig. 11.7), where it was detected until 29/11/2009 and then recaptured within the vicinity on the 2/12/2009 (Table A11.2). Also, for Fish 229 that was captured and tagged at the *Illusion* on 11/11/2009 and for which there was only a single detection, it was recaptured at Plank Shoal four months later on 13/03/2010.

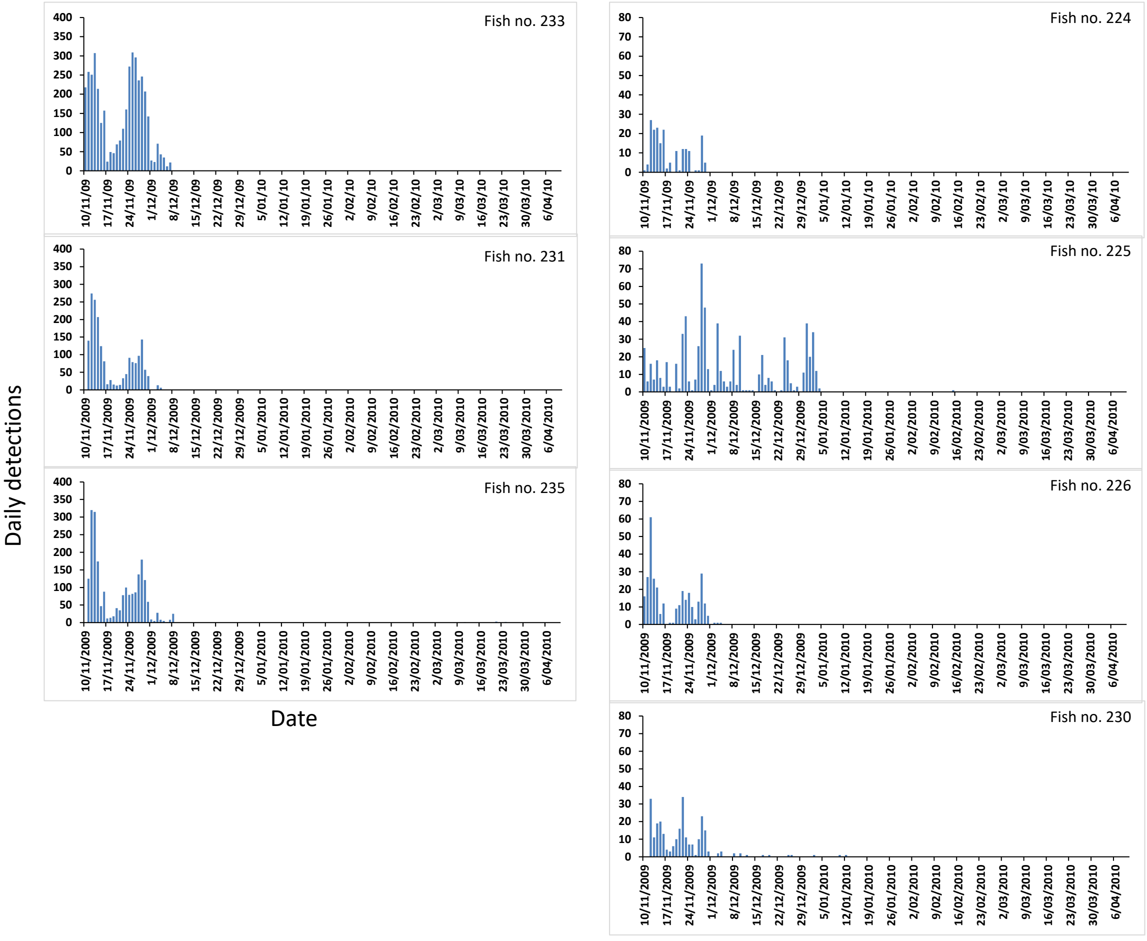

Fig. 11.6. Daily detections for seven fish recorded in the acoustic telemetry study in Northern Spencer Gulf between 10th November 2009 and 10th April 2010. Left hand graphs relate to fish tagged and detected at Plank Shoal, right hand graphs to those tagged and detected at the *Illusion*. Note the different scales of the Y-axes between the left hand and right hand graphs.

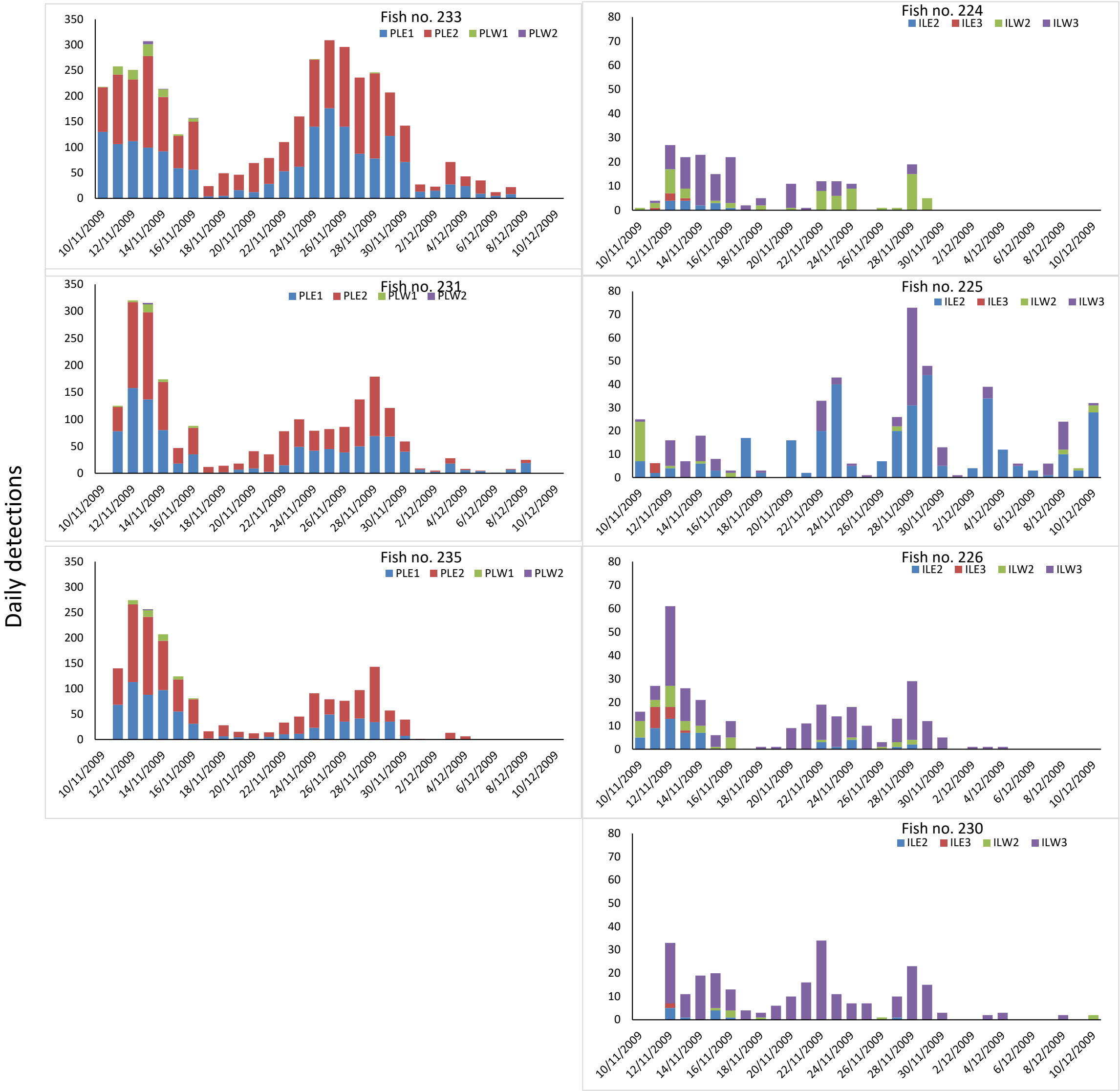

Fig. 11.7. Daily detections between 10th November 2009 and 10th December 2009 for seven fish recorded in the acoustic telemetry study in Northern Spencer Gulf. Left hand graphs relate to fish tagged and detected at Plank Shoal, right hand graphs to those tagged and detected at the *Illusion*. Note the differences in the scale of the Y-axes between the left hand and right hand graphs.

11.3.2 Northern Gulf St. Vincent

Across the approximate three years of this project, there were 521,567 detections, of which 521,544 were recorded in the study area in NGSV. The remaining 23 were recorded from a single fish along the Glenelg line of receivers in October 2012 and January 2013 (Fig. 11.3a). The numbers of detections per fish varied considerably, ranging from zero to 67,040 (Table A11.4, Fig. 12.8a). Seven fish produced no detections and for 14 fish there were <500 detections. In contrast, for 15 fish there were >10,000 detections. The detection periods were highly variable, ranging from zero to 867 days (Table A11.4, Fig. 11.8b). For 31 fish, the detection period exceeded 100 days, and for 19 fish was greater than one year. Overall, there was variation in detection rate and detection periods amongst the tagged fish, indicating they used the study area in different ways.

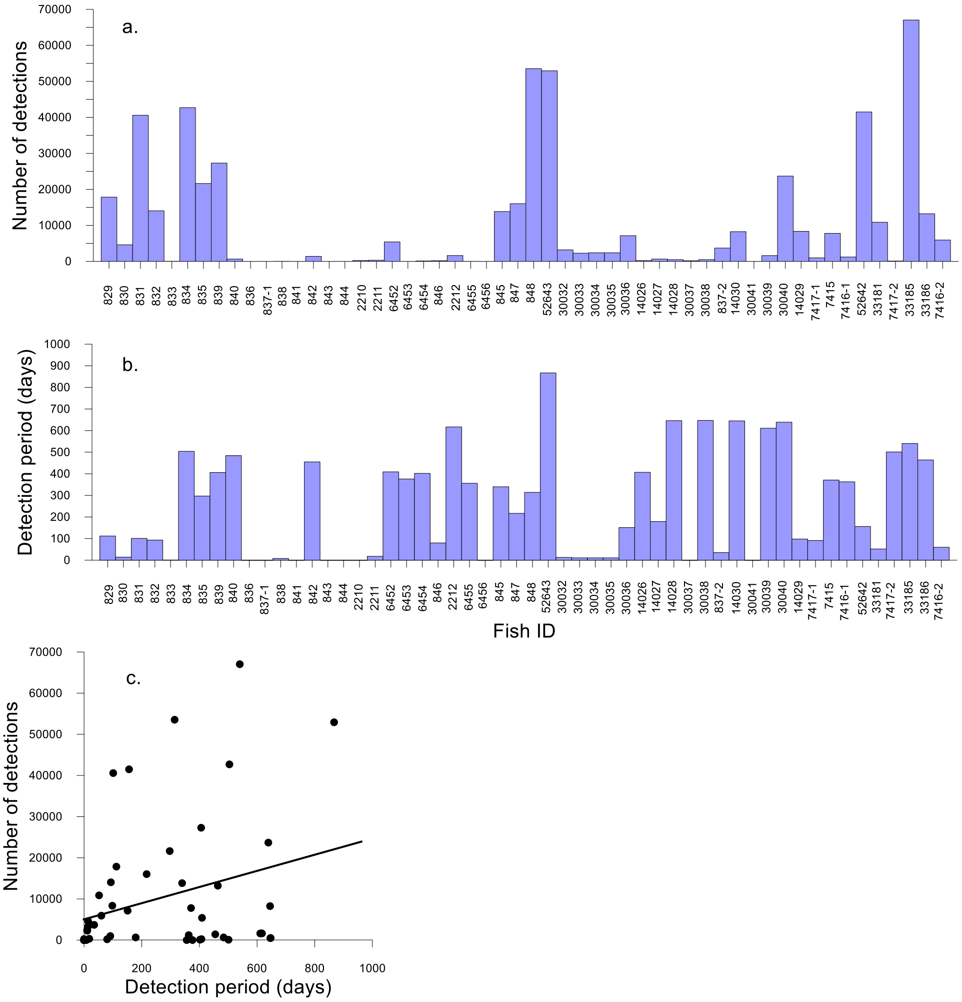

Fig. 11.8. Summary of results from the acoustic telemetry study in NGSV. a. number of detections recorded for each tagged fish in the order in which they were tagged; b. detection period in days for each fish; c. relationship between number of detections and detection period, showing the significant linear relationship.

Space use – timing and duration of occupancy of study area

The BP area produced no detections from May 2011 and was difficult to work, so was not considered after April 2012. For the other five areas, the detections of tagged Snapper were uneven, but spatially consistent amongst years (Fig. 11.9a). The ZN area accounted for 67.8% of all detections across the three years, followed by 25.4% at LS, with the remaining 6.8% accounted for by decreasing contributions from AR, AG and AN, respectively. The uneven spatial contribution of detections related partly to differences in the numbers of Snapper detected per area. These were marginally higher at ZN compared to several other areas (Fig. 11.9b). However, the uneven spatial contribution of detections was primarily driven by huge differences in the rates of detections per viable fish per receiver. These were several orders of magnitude higher in the ZN area than the other areas (Fig. 11.9c). This indicates that, on average, individual fish spent considerably longer periods in the ZN area than the other areas.

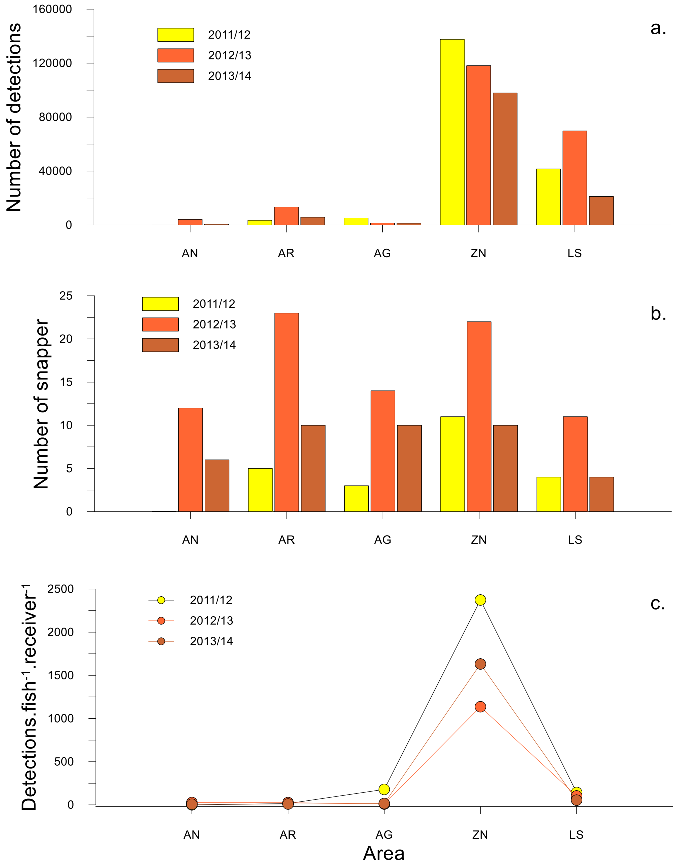

Fig. 11.9. Summary of spatial results from the acoustic telemetry study for Snapper in NGSV at the scale of area. a. number of detections recorded per year in the five areas where detections were recorded; b. number of Snapper detected per year in each area; c. number of detections per viable fish per acoustic receiver in each area.

The two areas with highest detections, i.e., ZN and LS, supported very different benthic habitats. The former was deep with largely bare substratum with razorfish distributed throughout (Fig. 11.5). The latter was shallower and dominated by a high cover of seagrass. Despite the high detections in the ZN area, the benthic habitat was similar to that in the AN, AR and AG areas. The primary habitat difference amongst these areas was the presence at 17ZN of the large wreck of the *Zanoni*.

When considered at the scale of station, 17ZN consistently accounted for the highest numbers of detections in each of the three years (Fig. A11.3a,b,c). Whilst the station was visited by the highest numbers of tagged Snapper annually (Fig. A11.3d,e,f), the average rates of detections were generally several orders of magnitude higher than for other stations (Fig. A11.3g). Station 24LS also consistently received high numbers of detections, whilst for 18BG and 27LS there were relatively high detections and detection rates in two of the three years.

Temporal analysis

The number of stations where fish were detected varied over time (Fig. 11.10). This probably reflects the influence of numerous factors that include the number of viable fish, as well as when and where they were tagged. Nevertheless, there were three periods when tagged Snapper were recorded at numerous stations, (i.e., through the spring/summer of 2012/13, the spring of 2013 and autumn 2014), suggesting when the fish were more active and mobile. The distribution of detections of individual fish over time relative to the tag dates and periods of viability of the tags indicates that no fish was ever detected continuously in the study area. Different fish were detected at different times and durations (Fig. 11.11). As such, the fish used the study area in different ways.

The numbers of detections across all tagged individuals for the study area and each of the five component areas were standardised according to the monthly SDFs. The standardised detection rate for the study area was highly variable amongst months, but with several modes in the time series, i.e., during the winters of 2011 and 2014, and the summers of 2011/12, 2012/13 and 2013/14 (Fig. 11.12a). These modes reflected seasonal differences in the spatial distribution of detections. For the four areas of AN, AR, AG and LS, the detection rates were highest during spring and summer (Fig. 11.12b,c,d,f). In contrast, high rates of detections in the ZN area were responsible for winter peaks in both 2011 and 2014 (Fig. 11.12e). This area also had high detections in spring and summer of 2012/13. The distribution of detections over time indicates that the dispersion of the fish changed seasonally. In summer, they were more broadly dispersed and detected at more stations, again suggesting that the fish were active and mobile at this time of the year.

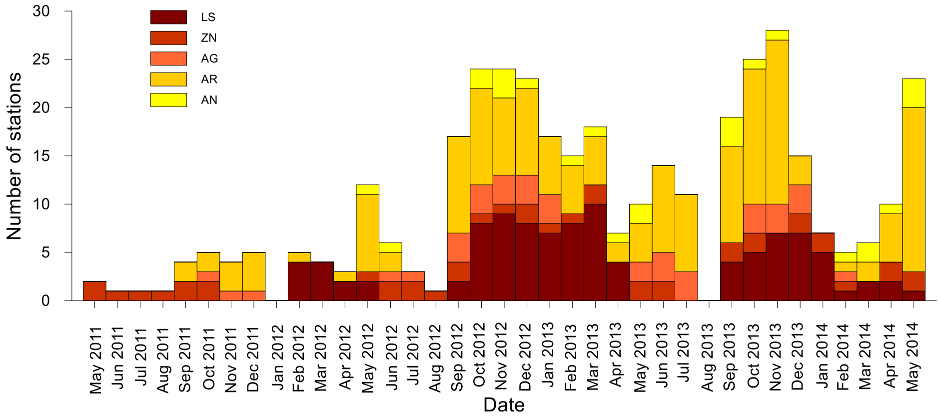

Fig. 11.10. Total number of stations in the study area in NGSV at which tagged Snapper were detected per month across the three-year study period.

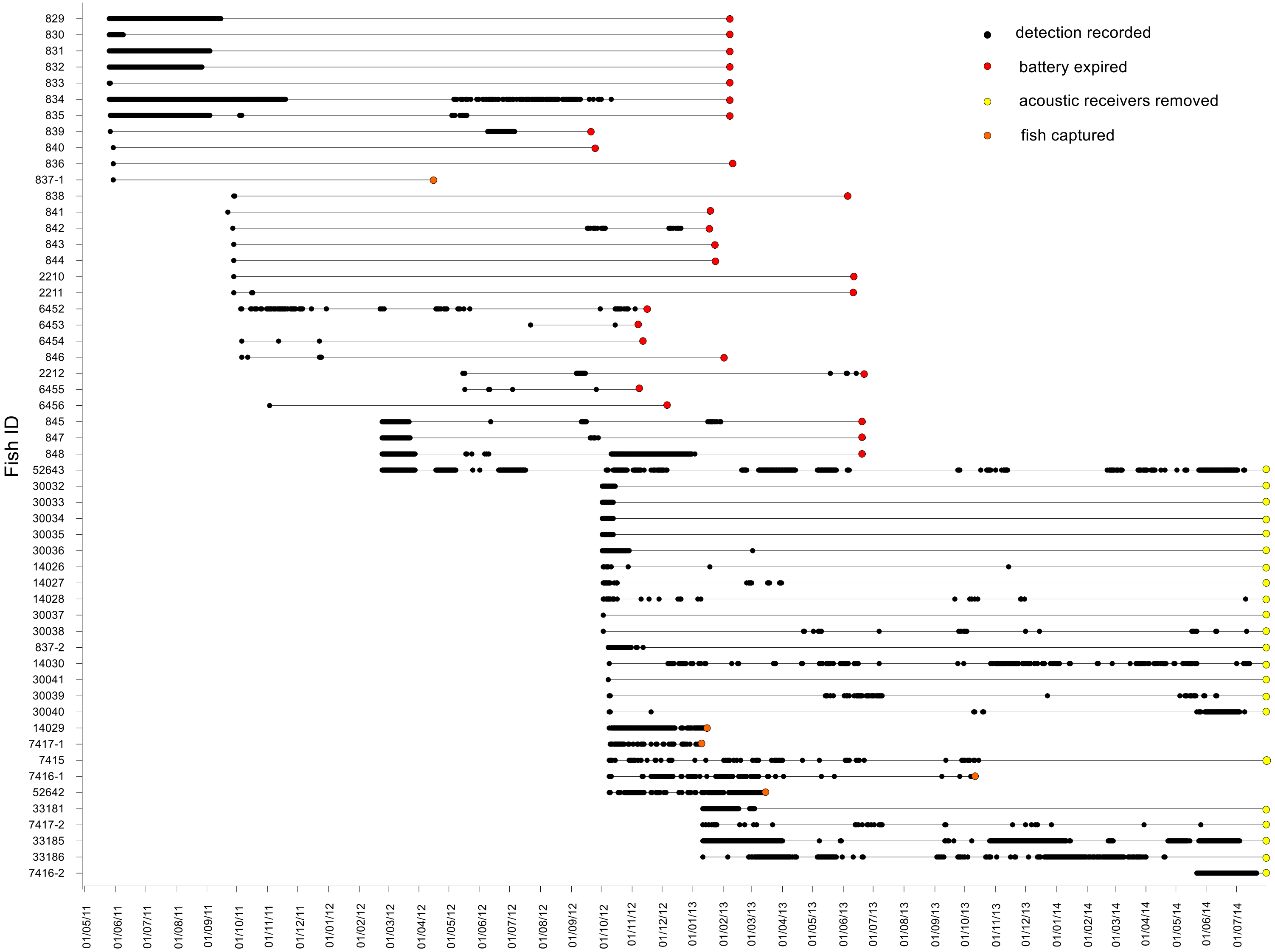

Fig. 11.11. Timing of the detections of the tagged fish in the acoustic telemetry study from when first tagged to either when the battery expired, the fish was captured or the study was terminated.

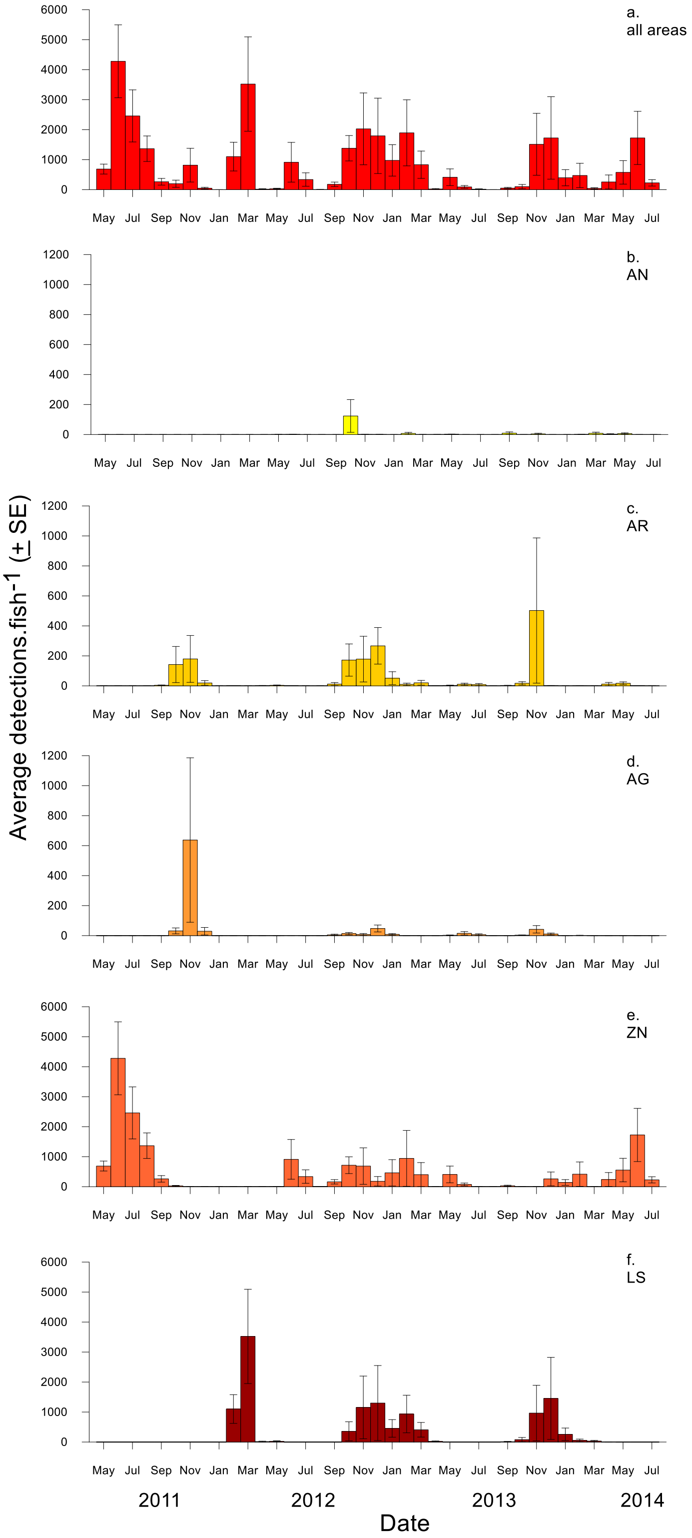

Fig. 11.12. Summary of spatial and temporal results from the acoustic telemetry study for Snapper in NGSV. a. estimates of monthly detection rates across the whole study area for the duration of the study from May 2011 until July 2014. b, c, d, e, f show the monthly detection rates per viable fish for each component area for the duration of the study. Note the different scales on the Y-axes for different areas.

11.4 Discussion

11.4.1 Northern Spencer Gulf

This chapter considered two of the three acoustic telemetry studies that have been done for Snapper in South Australia. The first study, done in NSG, provided some insights into their space use and behaviour. This five-month study involved ten acoustic receivers that were used at two Snapper aggregation sites located 5 nm apart. Thirteen Snapper across a broad size range were caught and tagged in the vicinity of the two small arrays of receivers. There was a total of 9,605 detections, mostly provided by seven fish. These were detected daily for approximately three weeks after tagging, but not continuously through this period. This suggests that they undertook daily movements outside the range of the receivers, before subsequently returning. Also, as some receivers consistently had more detections than others, indicates that the fish returned to and occupied the same small areas in the vicinity of the acoustic arrays. So, through this period, the tagged Snapper displayed systematic, localised behaviour throughout which they were relatively sedentary and site-attached.

For the three weeks between when the fish were tagged and when the fishery reopened on the 30th November 2009, there were several periods between which the detection rates and different depth zones were occupied. These suggest that the behaviour of the fish changed between the two periods. These activities may have related to spawning activity as well as to the times that the fish spent foraging. The different periods were most obvious for the three fish from Plank Shoal that accounted for most detections. During the first period from 11 to 16th November, the high numbers of detections indicated that the fish stayed in the vicinity of the Plank Shoal Light, at relatively deep depth zones. For the second period from the 17th to 21st November far fewer detections were recorded suggesting that the fish spent less time in the vicinity of the array. When there, they occupied marginally shallower depths. The third period from 22nd to 30th November involved high numbers of detections, the occupation of shallower waters and the cyclical, diurnal behaviour of movement over broad depth ranges.

From the 1st December 2009 onwards, for six of the seven fish, there were only incidental numbers of detections. The reductions in detection rates from this date reflects that for extensive periods these fish moved outside of the vicinity of the arrays at Plank Shoal and the *Illusion*. This was the time that the fishery reopened after the month-long closure throughout November. The opening day of the fishery generally involved considerable activity of commercial and recreational fishers, with the *Illusion* known to attract large numbers of fishers, involving many fishing vessels. This would have created considerable activity at the surface, resulting in noise throughout the water column. The coincidence in timing of the change in behaviour of the fish with the reopening of the fishery, strongly implies a strong disturbance effect on the fish.

11.4.2 Northern Gulf St. Vincent

The second acoustic telemetry study that was undertaken in NGSV involved considerable increases in the spatial and temporal scales compared to the first study in NSG. Over the three years of this study, up to 41 acoustic receivers were deployed throughout an area of approximately 160 km^2. A total of 54 Snapper, from across a broad size range, were tagged with acoustic tags, with from 11 to 46 viable fish at any one time. There were 521,544 detections recorded within the study area and a further 23 recorded in southeast Gulf St. Vincent. The use of space by the tagged fish was assessed by comparing the timing and duration of detections at the various stations and areas. No fish was detected continuously throughout its detection period. Rather, there was considerable variation in the frequency and duration of their visits to the study area. These were indicative of several categories of behaviour with respect to how the study area was used. For 10 fish, either no or only a small number of detections were recorded up to a day or two after being tagged. The fate of most of these is unknown and may have ranged from simply remaining outside the study area to being caught by a fisher. Alternatively, the fate of Fish 837-1 was known as it was recaptured over 10 months later by a recreational fisherman near where it had been tagged. The remaining 44 fish were detected a sufficient period after tagging to know that they had survived the tagging process. The numbers and temporal patterns of detections varied considerably amongst fish, reflecting different ways that the fish used the study area.

Temporary residents

'Temporary residents' were detected daily at the same station for between several weeks and four months at a time. This behaviour was only recorded at station 17ZN, where the largely intact shipwreck of the *Zanoni* remains a large, submerged structure. These fish contributed large numbers of detections, did not venture far from the shipwreck, and showed considerable overlap in their use of space amongst individuals. This sedentary space use was only evident for 'small' and 'medium' sized fish and was only recorded during winter and early spring in the vicinity of the shipwreck. So, at this time of the year, these fish showed strong site fidelity, and had long periods of occupancy around the shipwreck. These findings are consistent with anecdotal reports from fishers that relatively small Snapper remain close to the wreck (Lloyd pers. comm.).

For small to medium-sized Snapper, the characteristics of limited and overlapping home ranges and strong site fidelity have been described from acoustic telemetry studies done in New Zealand and New South Wales (Willis et al. 2001, Hartill et al. 2003, Parsons et al. 2003, Parsons et al. 2010, Harasti et al. 2015). The difference in findings between those studies and this one is that here such 'residential' behaviour did not persist into the warmer months. In NGSV, the frequencies of detections declined through August and September, indicating that the time that the fish spent in the vicinity of the shipwreck declined until early spring when the detections ceased altogether. Most of these fish were detected for only one prolonged period. After leaving 17ZN, several moved north over distances of km to 10's of km to the AR and AN areas, a significant seasonal change in space use but not necessarily a significant shift in benthic habitat. Rather, the primary habitat change was that the fish moved away from the vicinity of the shipwreck. Commercial fishers have indicated that the fish need to move to find new foraging grounds.

Mobile, partial residents

The other behavioural category for which there were large numbers of detections for individual fish that spent considerable periods of time in the study area were the ‘mobile, partial residents’. In contrast to the ‘temporary residents’, the detections of these fish were generally distributed across several areas and numerous stations that were considerable distances apart. This involved a relatively large scale of movement compared to findings of earlier, small-scale movement studies done in New Zealand (Willis et al. 2001, Hartill et al. 2003, Parsons et al. 2003, Parsons et al. 2010) and New South Wales (Harasti et al. 2015). These fish were in the ‘large’ and ‘very large’ size classes and displayed seasonal variation in behaviour and areas used (Fig. 11.13). For periods during winter, some were detected daily at 17ZN. In this sense, this was like that of the ‘temporary residents’, although their periods of residence at 17ZN were generally shorter. In spring, they moved and were detected throughout the AN, AR and AG areas, giving the highest detection rates in these areas. Also, during spring, some fish moved to the LS area, where they stayed until late summer. For periods of several weeks during these warmer months, the daily activity of these fish occurred over areas that were monitored by several acoustic stations. As such, these ‘local’ movements occurred over greater distances and throughout broader areas than the fish moved during winter.

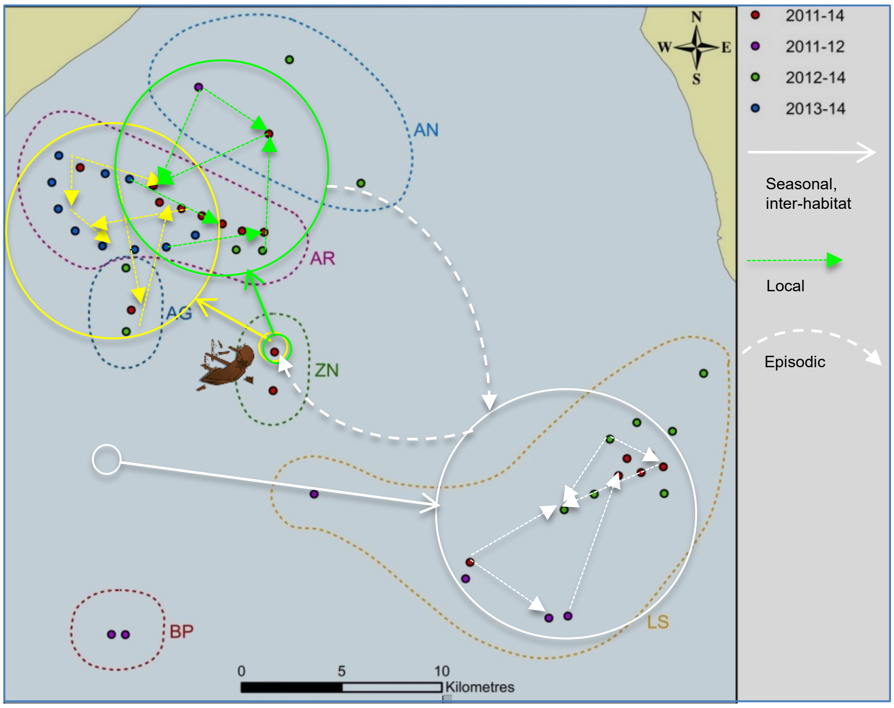

Fig. 11.13. Model of the movement behaviour of snapper in NGSV for three hypothetical fish (green, yellow, white). The figure depicts the areas occupied by each fish during winter and spring/summer and the direction of the ‘seasonal, inter-habitat’ movement between winter and spring. The ‘local’ and ‘episodic’ movements that occur during summer are also depicted.

During spring and summer after these fish had dispersed to the AN, AG and AR areas and their daily movements were extensive enough to be detected at several different stations, their activity was occasionally punctuated by significant excursions to different places (Fig. 11.13). Here, such excursions generally involved movements between areas, over distances of 10s of km in less than a single day. Sometimes the fish completed the round trip back to the original site. Such behaviour generally occurred prior to or during the reproductive season in the northern gulfs. It may have related to seasonal gonad maturation and reproductive behaviour. Movement studies for other species of large, demersal fish that normally occupy limited home ranges have demonstrated the spontaneous movement of individuals over distances of 10s of km, to participate in spawning aggregations (Zeller 1998, Starr et al. 2007).

Transient, infrequent visitors

For some fish there were few detections recorded in the study area. This indicates that they only occasionally strayed into or passed through the study area. As such, they are here called ‘transient, infrequent visitors’. These were primarily ‘large’ fish. It is impossible to interpret such observations in any comprehensive description of movement. Nevertheless, their behaviour may not have necessarily differed from that described above for the ‘mobile, partial residents’, but with their centres of activity located near but outside the study area. The same could apply to those fish for which no detections were recorded as most had been captured and tagged considerable distances away, and the scope of their movements may not have extended into the study area.

Movement behaviour

Several different types of movement behaviour by Snapper were implicit in the patterns of space use as described above. These were characterised by the distances moved by the fish, the timing of their movement and places involved (Fig. 11.13). These can be categorised as: inter-regional; seasonal movement; local movement; and episodic movement.

Two of the large, tagged fish demonstrated inter-regional movement between the study area in NGSV and either the central or southern parts of Gulf St. Vincent. They moved over the longest linear distances recorded in the study. Fish 14026 was captured, tagged, and first recorded in the northern gulf but was later recorded on the Glenelg line of receivers. By the following year it had returned to the northern gulf. The linear distance between the furthest stations visited was approximately 82 km. Fish 842 was the southern-most fish captured and tagged. The distance between the tag site and the furthest site of detection was 64 km. For both fish, these are linear distances between detection points and so under-represent the actual distances that they would have moved during their detection periods. This exchange of individuals between the northern and southern parts of the gulf indicates that the population in NGSV is not an isolated, self-contained stock that is separated from the southern gulf. In this sense this contrasts with the limited movement behaviour that is characteristic of the different gulfs in Shark Bay, Western Australia (Bastow et al. 2002, Norriss et al. 2012).

At the smaller, within-region scale it is possible that there are differences in the movement behaviour of small and large Snapper. During winter, numerous fish were relatively sedentary at Station 17ZN for periods of up to several months. This is consistent with reports from commercial fishers of large schools of Snapper at Black Point during winter 2013 and around the wreck of the *Zanoni* during winters of 2014 and 2015. Such reports indicate that these schools are not necessarily always associated with the wreck of the *Zanoni*, despite it being a large structure in the northern gulf. The fish undergo a seasonal behavioural change associated with a spatial shift during late winter and spring, when they disperse from winter schools and quickly move several kilometres to places in the AN, AR and AG areas. Such places are dominated by silt and sand benthos, with relatively low cover of algae and seagrass, and benthic invertebrates particularly razorfish (Tanner 2005). Throughout such areas the preferred prey taxa of Snapper, such as blue swimmer crabs (Lloyd 2010), are also common. As such, the seasonal movement and habitat shift of Snapper is likely to relate, at least in part, to dietary requirements. During spring and summer, the fish were more mobile than during winter. They occupied areas for several weeks at a time during which their daily activities occurred throughout areas that were sufficiently large to be detected by several acoustic receivers. Such 'local' activity concentrated in certain areas was occasionally interrupted by abrupt, episodic, movements over distances of 10s of km that may have been associated with reproductive activity (Fig. 11.13).

11.4.3 Conclusions

The two acoustic studies described here were useful in providing insights into the space use and movement behaviour of Snapper at relatively small spatial and temporal scales in the northern gulfs. The acoustic studies demonstrated that the space use of Snapper in such environments can be relatively sedentary and site-attached for periods of time. This was apparent in NSG during the reproductive season in spring/ early summer, as well as during summer and winter in NGSV. Such findings are consistent with those from acoustic telemetry studies done in New Zealand and New South Wales (Willis et al. 2001, Hartill et al. 2003, Parsons et al. 2003, Parsons et al. 2010, Harasti et al. 2015). However, in South Australia, the site-attached nature of the fish did not persist. Both in NSG and NGSV, the fish did not remain aggregated, and they eventually moved away from the aggregation sites. The reasons for this are likely to have differed between the studies, i.e., potentially reflecting an anthropogenic influence on fish behaviour in NSG, and natural seasonal movement in NGSV. In the latter study, the fish generally occupied small areas for weeks to months at a time. However, the areas differed between seasons and were separated by distances of up to tens of kilometres. As fish used different areas throughout the year, their overall activity patterns could be distributed over areas of hundreds of square kilometres. The local site-attached nature of the space use was most evident around large structures such as the shipwrecks and navigation light. Snapper are clearly thigmotaxic, which is manifested by them aggregating around such structures that rise above the seafloor. The *Zanoni*, which is a particularly large submarine structure, acted as a hub for Snapper behaviour, where the fish aggregated for periods of time or where they stopped temporarily as they moved between other places.

The study in NGSV identified several different types of fish movement that differed in their timing and spatial scale. It demonstrated that the Snapper were highly mobile and exhibited systematic behaviour at several temporal scales and showed refined skills of navigation. Some fish moved over straight-line distances that approached 100 km and could move tens of km in a single day. This broader scale movement was not apparent in previous acoustic telemetry studies. It may be idiosyncratic to South Australia, because of the different habitats occupied compared to those considered in other studies (i.e., soft benthos dotted with numerous artificial reefs compared to reef habitat). The systematic nature of the behaviour was evident in that the fish undertook repeat visits to the same places, which occurred at different temporal scales ranging from daily to annual. It reflects that the fish had the ability to move between and to find places, sometimes very quickly, that were distributed throughout areas of hundreds of square kilometres.

Previous movement studies for Snapper in the coastal waters of South Australia were based on tag/recapture (Jones 1981, 1984) or otolith chemistry (Fowler et al. 2016, 2017) and were informative at inter-regional and inter-annual spatial and temporal scales. The findings of the acoustic telemetry studies can be considered in the light of those historical tag/recapture studies (Jones 1981, 1984, McGlennon 2003). There are consistencies between studies, as well as additional information provided by each. The acoustic telemetry study in NGSV identified seasonal and size-related changes in fish behaviour. During winter, fish across the size range of small to very large were schooled up and were relatively sedentary for weeks to months. In late winter and spring, the schools dispersed. Their subsequent behaviour may have been size-related. Few ‘small’ and ‘medium’ fish were detected throughout the study area during the warmer months. This is consistent with observations from tag/recapture studies that the smaller fish moved south and possibly left the gulfs. In contrast, most acoustic detections throughout the warmer months involved large and very large fish, which according to earlier studies tended to stay in the northern gulfs (McGlennon 2003). This acoustic telemetry study provided insight into the behaviour of these fish during the warmer months that had not been attainable in the earlier studies. Their activities at these times fell into the ‘local’ and ‘episodic’ movement categories. It is important to note that the fish movement studies that used external tagging identified that most recaptures across all size classes, including small fish, were made within only a few nautical miles of their release sites, and so should be considered ‘residents’. However, of the fewer fish that did undertake significant movements (i.e., the ‘migrants’), most were smaller fish (McGlennon 2003). From this, it is tempting to suggest that most ‘mobile, partial residents’ and even the ‘transient, infrequent’ visitors to our study area were residents of NGSV even though they were not continuously recorded within the study area.

11.5 References

Andrewartha, H.G., Birch, L.C. (1954). The distribution and abundance of animals. University of Chicago Press, Chicago.

Baker, J.L. (2000). MPA Design and selection: numerous approaches, no consensus. Chapter 6 in Guide to Marine Protected Areas. Report to South Australian Department for Environment and Heritage. 201pp.

Bastow, T.P., Jackson, G., 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 11(5), 801-806.

Brown, J.L., Orians, G.H. (1970). Spacing patterns in mobile animals. Annual Reviews in Ecology and Systematics 1: 239-262.

Crossland, J. (1976). Snapper tagging in north-east New Zealand, 1974: analysis of methods, return rates, and movements. New Zealand Journal of Marine and Freshwater Research 10: 675-686.

Egli, D.P., Babcock, R.C. (2004). Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus auratus*) in a temperate no-take marine reserve. ICES Journal of Marine Science 61: 1137-1143.

Fowler, A.J., Gillanders, B.M., Hall, K.C. (2005). 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, R., Burch, P., Feenstra, J.E., Jackson. W.B. (2010). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-2, SARDI Research Report Series No. 473. Pp 109.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E., Jackson. W.B., Lloyd, M.T. (2013). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-3, SARDI Research Report Series No. 713. 103pp.

Fowler, A.J., McGarvey, R., Carroll, J., Feenstra, J.E., Jackson, W.B., Lloyd, M.T. (2016). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-4. SARDI Research Report Series No. 930. 82pp.

Fowler, A.J., Hamer, P.J., Kemp, J. (2017). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely-dispersed, coastal fishery species. Fisheries Research 189: 77-94.

Hamer, P.A., Jenkins, G.P., Gillanders, B.M. (2005). Chemical tags in otoliths indicate the importance of local and distant settlement areas to populations of a temperate sparid, *Pagrus auratus*. Canadian Journal of Fisheries and Aquatic Sciences 62: 623-630.

Hamer, P.A., Jenkins, G.P., Coutin, P. (2006). Barium variation in *Pagrus auratus* (Sparidae) otoliths: a potential indicator of migration between an embayment and ocean waters in south-eastern Australia. Estuarine, Coastal and Shelf Science 68: 686-702.

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Harasti, D., Lee, K.A., Gallen, C., Hughes, J.M., Stewart, J. (2015). Movements, home range and site fidelity of Snapper (*Chrysophrys auratus*) within a temperate marine protected area. Plos ONE 10(11):e0142454. doi:10.1371/journal.pone.0142454.

Hartill, B.W., Morrison, M.A., Smith, M.D., Boubée, J., Parsons, D.M. (2003). Diurnal and tidal movements of snapper (*Pagrus auratus*, Sparidae) in an estuarine environment. Marine and Freshwater Research 54: 931-940.

Heupel, M.R., Webber, D.M. (2012). Trends in acoustic tracking: where are the fish going and how will we follow them? American Fisheries Society Symposium 76: 219-231.

Heupel, M.R., Semmens, J.M., Hobday, A.J. (2006). Automated acoustic tracking of aquatic animals: scales, design and deployment of listening stations. Marine and Freshwater Research 57: 1-13.

Huveneers, C., Rogers, P.J., Drew, M. (2012). Monitoring shark species of conservation concern within the Adelaide metropolitan region. Final Report to the Adelaide & Mount Lofty Ranges Natural Resources

Management Board. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2012/000246-1. SARDI Research Report Series No. 664. 35pp.

Jones, G.K. (1981). Biological research on snapper (*Chrysophrys auratus* syn. Unicolor) and an analysis of the fishery in Northern Spencer Gulf. SAFISH 5-8.

Jones, G.K. (1984). A review of the commercial fishery for snapper (*Chrysophrys auratus*) in South Australian waters. Discussion paper, Department of Fisheries, South Australia. November 1984.

Kailola, P.J., Williams, M.J., Stewart, P.C., Reichelt, R.E., McNee, A., Grieve, C. (1993). Australian Fisheries Resources. Bureau of Resource Sciences and the Fisheries Research and Development Corporation, Canberra Australia. Imprint Limited, Brisbane.

Kingett, P.D., 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.

Lloyd, M.T. (2010). Spatial variation in growth of snapper (*Chrysophrys auratus*) in South Australian gulf waters: an investigation of diet as a contributing factor. Honours thesis – Adelaide University. 66pp.

McGlennon, D. (2003). The fisheries biology and population dynamics of snapper *Pagrus auratus* in northern Spencer Gulf, South Australia. PhD thesis. Department of Environmental Biology, University of Adelaide, Australia. 219pp.

Moran, M., Burton, C., 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.

Parsons, D.M., Babcock, R.C., Hankin, R.K.S., Willis, T.J., Aitken, J.P., O'Dor, R.K., Jackson, G.D. (2003). Snapper *Pagrus auratus* (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. Marine Ecology Progress Series 262: 253-265.

Parsons, D.M., Morrison, M.A., Slater, M.J. (2010). Responses to marine reserves: decreased dispersion of the sparid *Pagrus auratus* (snapper). Biological Conservation 143: 2039-2048.

Paul, L.J. (1967). An evaluation of tagging experiments on the New Zealand snapper, *Chrysophrys auratus* (Forster), during the period 1952 to 1963. New Zealand Journal of Marine and Freshwater Research 1: 455-463.

Payne, N.L., Gillanders, B.M., Webber, D.M., Semmens, J.M. (2010). Interpreting diel activity patterns from acoustic telemetry: the need for controls. Marine Ecology Progress Series 419: 295-301.

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.

Shepherd, S.A, Sprigg, R.C. (1976). Substrate, sediments and subtidal ecology of Gulf St. Vincent and Investigator Strait. In: Natural history of the Adelaide Region: edited by C.R. Twidale, M.J. Tyler, and B.P. Webb. Royal Society of South Australia, Adelaide. Pp.161-174.

Starr, R.M., Sala, E., Ballesteros, E., Zabala, M. (2007). Spatial dynamics of the Nassau grouper *Epinephelus striatus* Caribbean atoll. Marine Ecology Progress Series 343: 239-249.

Sumpton, W.D., Sawynok, B., Carstens, N. (2003). Localised movement of snapper (*Pagrus auratus*, Sparidae) in a large subtropical marine embayment. Marine and Freshwater Research 54: 923-930.

Tanner, J.E. (2005). Three decades of habitat change in Gulf St. Vincent, South Australia. Transactions of the Royal Society of South Australia 129: 65-73.

Willis, T.J., Parsons, D.M., Babcock, R.C. (2001). Evidence for long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve. New Zealand Journal of Marine and Freshwater Research 35: 581-590.

Zeller, D.C. (1998). Ultrasonic telemetry: its application to coral reef fisheries research. Fishery Bulletin 97: 1058-1065.

11.6 Appendices

Table A11.1. Details of the deployment of acoustic receivers in Northern Spencer Gulf in 2009/10.

Station	Site	Receiver ID	Date deployed	Time deployed	Latitude	Longitude	Depth (m)
ILE1	*Illusion*	102318	9/11/2009	13:50	33.28.742	137.33.081	11.2
ILE2	*Illusion*	101047	9/11/2009	14:10	33.28.948	137.32.862	13.5
ILE3	*Illusion*	100982	9/11/2009	14:28	33.29.156	137.32.670	15.8
ILW3	*Illusion*	100980	9/11/2009	14:39	33.28.901	137.32.439	16
ILW2	*Illusion*	101041	9/11/2009	14:50	33.28.686	137.32.628	16.1
ILW1	*Illusion*	101048	9/11/2009	15:01	33.28.508	137.32.853	17.3
PLE1	Plank Light	102317	10/11/2009	8:50	33.29.751	137.28.645	12.9
PLE2	Plank Light	101042	10/11/2009	9:02	33.30.020	137.28.638	12.9
PLW2	Plank Light	101039	10/11/2009	9:14	33.30.048	137.28.308	12.8
PLW1	Plank Light	101043	10/11/2009	9:25	33.29.752	137.28.311	

Table A11.2. Details of the fish tagged with acoustic tags for the acoustic telemetry study done in Northern Spencer Gulf in 2009/10.

Fish no.	Fish size CFL (cm)	Date tagged	Time tagged	Site	Date first detected	Date last detected	Recapture date	Recapture site	Time at liberty (days)	No. detections
233	76	10/11/2009	10:45	Plank	10/11/09	7/12/09				4,008
224	67	10/11/2009	12:37	Plank	10/11/09	29/11/09	2/12/09	*Illusion*	22	194
225	33	10/11/2009	13:15	*Illusion*	10/11/09	15/02/10				734
232	37	10/11/2009	13:17	*Illusion*						0
226	39	10/11/2009	13:46	*Illusion*	10/11/09	4/12/09				317
235	66	11/11/2009	11:29	Plank	11/11/09	4/12/09				1,847
227	30	11/11/2009	12:31	Plank			27/12/09	Plank	46	0
231	44	11/11/2009	12:41	Plank	11/11/09	24/03/10				2,206
236	69	11/11/2009	13:38	Plank						0
228	75	11/11/2009	13:50	Plank	11/11/09	02/02/10				12
237	66	11/11/2009	14:35	Plank	11/11/09	11/11/09				23
229	70	11/11/2009	16:10	*Illusion*	12/11/09	12/11/09	13/03/10	Plank	122	1
230	31	11/11/2009	18:05	*Illusion*	12/11/09	12/01/10				263

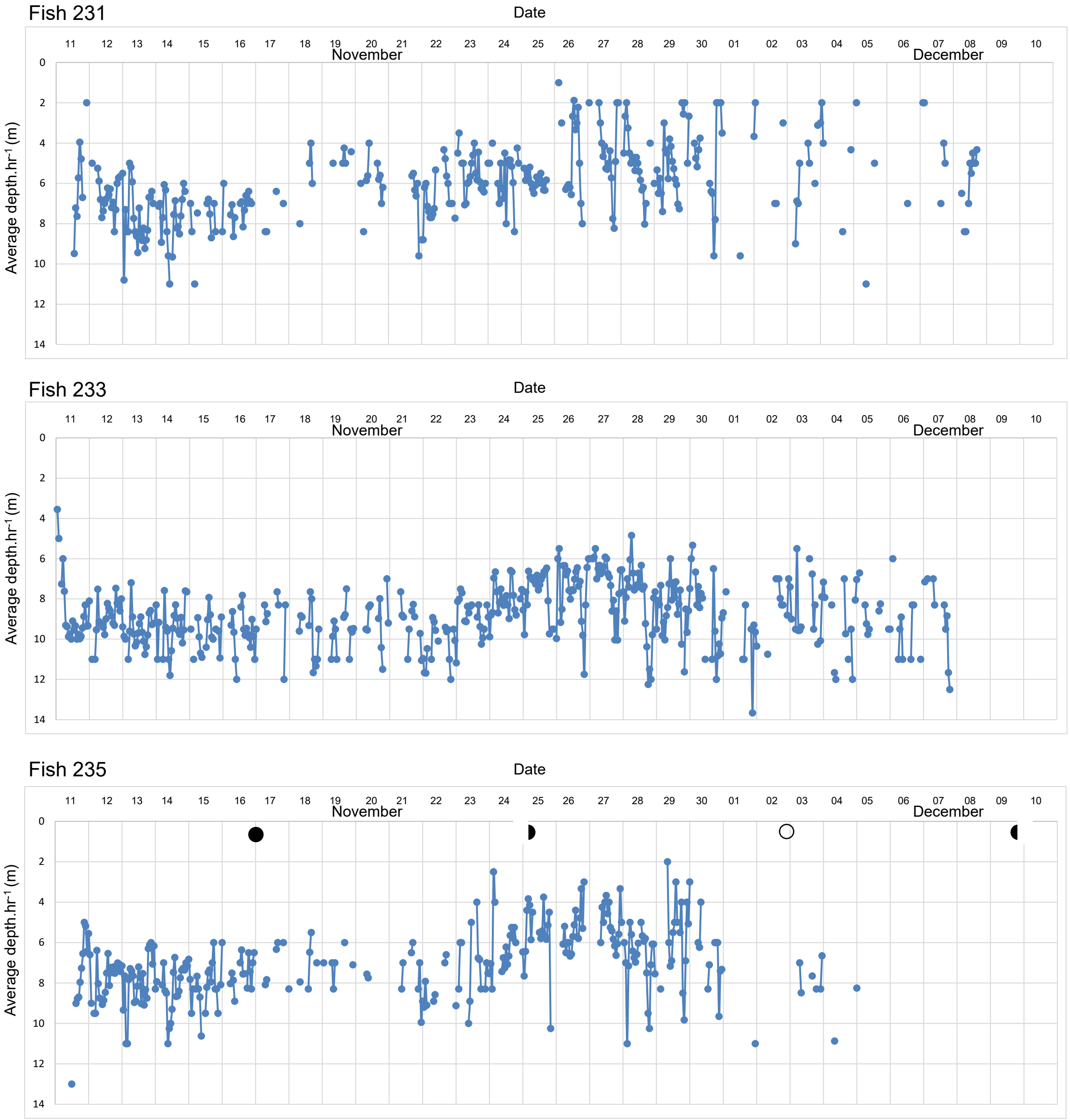

Fig. A11.1. Summary of depth data recorded during the acoustic telemetry study in NSG between 11th November and 10th December 2009 for three fish tagged at Plank Shoal. Data show the average depth at which each fish was recorded per hour. Where there are gaps in the data no detections were recorded at those times.

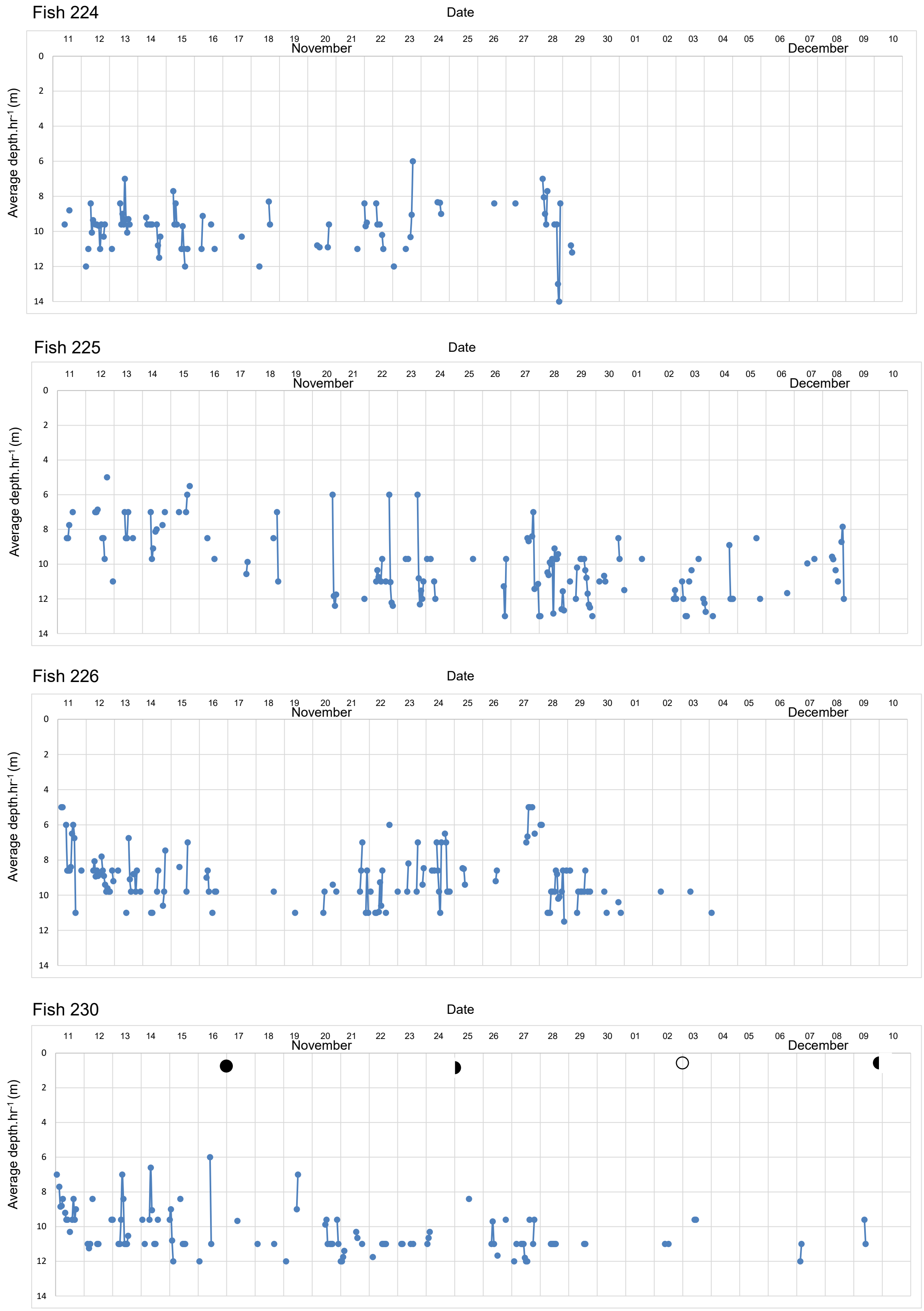

Fig. A11.2. Summary of depth data recorded during the acoustic telemetry study in NSG between 11th November and 10th December 2009 for four fish tagged at the *Illusion*. Data show the average depth at which each fish was recorded per hour. Where there are gaps in the data no detections were recorded at those times.

Table A11.3. Information relating to deployment of acoustic receivers in NGSV from May 2011 until May 2014. Information includes; Station name and Area in which it was located, the depth where deployed, and the dates of deployment and/or termination. (Y – receiver deployed successfully). For relative locations of areas refer to Fig. 5.2.

Station	Area	Depth (m)	May 2011	April/May 2012	May 2013
4AN	AN	14.8	Y	Terminated	
2AN	AN	15.6	Y	Y	Y
4AR	AR	14.8	Y	Y	Y
5AR	AR	15.9	Y	Y	Y
6AR	AR	16.2	Y	Y	Y
7AR	AR	16.7	Y	Y	Y
8AR	AR	16.8	Y	Y	Y
9AR	AR	16.5	Y	Y	Y
10AR	AR	16.7	Y	Y	Y
11AR	AR	16.4	Y	Y	Y
15AG	AG	17.3	Y	Y	Y
17ZN	ZN	16.2	Y	Y	Y
18BG	ZN	17.5	Y	Y	Y
47BP	BP	22	Y	Missing	
48BP	BP	18.8	Y	Terminated	
LS7	LS	17.8	Y	Terminated	
LS8	LS	20.1	Y	Terminated	
LS9	LS	20.4	Y	Terminated	
LS10	LS	13.1	Y	Terminated	
23LS	LS	6.3	Y	Y	Y
24LS	LS	6.4	Y	Y	Y
25LS	LS	6.8	Y	Y	Y
26LS	LS	6.5	Y	Y	Y
27LS	LS	6.9	Y	Y	Y
31LS	LS	17.6	Y	Y	Y
1AN	AN	13.6		Y	Y
3AN	AN	13.5		Y	Y
12AR	AR	17.7		Y	Y
13AR	AR	18.1		Y	Y
14AG	AG	17.9		Y	Y
16AG	AG	19.3		Y	Y
19LS	LS	4.7		Y	Y
20LS	LS	9.3		Y	Y
21LS	LS	8		Y	Y
22LS	LS	9.7		Y	Y
28LS	LS	9.7		Y	Y
29LS	LS	9.5		Y	Y
30LS	LS	10.7		Y	Y
32AR	AR	17.3			Y
33AR	AR	18			Y
34AR	AR	18			Y
35AR	AR	16.7			Y
36AR	AR	15.4			Y
37AR	AR	15.6			Y
38AR	AR	16.0			Y
39AR	AR	17.0			Y
40AR	AR	18			Y
41AR	AR	17.2			Y

Table A11.4. Summary of results from the acoustic telemetry study done for snapper in NGSV. ('VP' refers to viable period for the battery). Spurious detections not shown.

Fish ID	CFL (cm)	Tag date	VP (days)	Date 1st detection	Date last detection	Detection period (days)	No. stations detected	No. areas detected	No. detections (all)	AN	AR	AG	ZN	LS	Days detected (all)	AN	AR	AG	ZN	LS
829	54	26/05/11	623	26/05/11	15/09/11	112	1	1	17848				17848		113				113	
830	40	26/05/11	623	26/05/11	9/06/11	14	1	1	4,599				4599		15				15	
831	46	26/05/11	623	26/05/11	4/09/11	101	1	1	40,587				40587		101				101	
832	39	26/05/11	623	26/05/11	27/08/11	93	1	1	14,044				14044		94				94	
833	36	26/05/11	623	26/05/11	27/05/11	1	2	1	26				26		2				2	
834	45	26/05/11	623	26/05/11	11/10/12	504	5	3	42,703		3360		38740	603	275		56		215	4
835	56	27/07/11	623	27/05/11	19/05/12	297	1	1	21,632				21632		115				115	
839	56	27/05/11	484	27/05/11	6/07/12	406	2	2	27,300	7			27293		29	1			28	
840	52	30/05/11	484	24/09/12	25/09/12	484	2	1	645				645		2				2	
836	50	30/05/11	623			0	0	0	0						0					
837-1	50	30/05/11	321			0	0	0	0						0					
838	47	21/09/11	623	28/09/11	29/09/11	8	2	2	16		13		3		2		1		1	
841	81	22/09/11	484			0	0	0	0						0					
842	74	22/09/11	484	17/09/12	20/12/12	455	13	3	1,396		806	411	179		20		14	8	2	
843	76	27/09/11	484			0	0	0	0						0					
844	89	28/09/11	484			0	0	0	0						0					
2210	53	28/09/11	623	28/09/11	28/09/11	0	1	1	255				255		1				1	
2211	45	28/09/11	623	28/09/11	16/10/11	18	2	1	318				318		3				3	
6452	85	5/10/11	399	5/10/11	17/11/12	409	9	3	5,402		62	5304	36		73		20	52	1	
6453	88	5/10/11	399	22/07/12	15/10/12	376	1	1	2			2			2			2		
6454	78	6/10/11	399	6/10/11	11/11/12	402	4	2	102		11	91			4		2	2		
846	80	6/10/11	484	6/10/11	25/12/11	80	3	2	197		102	95			5		2	3		
2212	68	6/10/11	623	15/05/12	14/06/13	617	7	3	1,627		14	13	1600		16		2	4	10	
6455	72	6/10/11	399	17/05/12	26/09/12	356	3	3	7		4	1	2		5		2	1	2	
6456	39	3/11/11	399			0	0	0	0						0					
845	80	24/02/12	484	24/02/12	29/01/13	340	9	3	13,839			15	838	12986	44			1	7	37
847	83	24/02/12	484	24/02/12	28/09/12	217	5	3	16,030		4		1875	14151	34		1		5	29
848	82	24/02/12	819	24/02/12	3/01/13	314	20	4	53,545	49	127			53369	123	2	4			117
52643	97	24/02/12	598	24/02/12	10/07/14	867	18	3	52,930		659		45179	7092	284	0	3		99	183
30032	48	2/10/12	598	2/10/12	15/10/12	13	4	3	3,199	194	4		3001		14	1	1		12	
30033	54	2/10/12	598	2/10/12	13/10/12	11	1	1	2,280				2280		12				12	
30034	42	2/10/12	598	2/10/12	13/10/12	11	1	1	2,393				2393		12				12	
30035	46	2/10/12	598	2/10/12	13/10/12	11	1	1	2,381				2381		12				12	
30036	45	2/10/12	598	2/10/12	2/03/13	151	1	1	7,142				7142		29				29	
14026	75	3/10/12	597	3/10/12	14/11/13	407	9	3	234		104	123		7	9		5	4		1
14027	65	3/10/12	597	3/10/12	31/03/13	179	6	3	646		192	1		453	22		11	1		11
14028	72	3/10/12	597	3/10/12	11/07/14	646	16	4	485	3	316	150	16		28	1	14	12	2	
30037	69	3/10/12	597	3/10/12	3/10/12	0	3	2	182		44		138		1		1		1	
30038	69	3/10/12	597	3/10/12	12/07/14	647	10	3	495	36	144		315		23	8	10		5	
837-2	48	8/10/12	320	8/10/12	12/11/12	35	1	1	3,698	3,698					27	27				
14030	82	8/10/12	592	9/10/12	15/07/14	645	26	4	8,255	468	4808	550	2429		144	31	71	26	22	
30041	80	8/10/12	592			0	0	0	0						0					
30039	65	9/10/12	591	9/10/12	12/06/14	611	19	3	1,616	44	712	860			49	5	22	29		
30040	64	9/10/12	591	9/10/12	10/07/14	639	16	4	23,689	1	558	6	23124		48	1	8	2	37	
14029	86	9/10/12	98	9/10/12	15/01/13	98	9	2	8,347		8304	43			89		85	6		
7417-1	80	9/10/12	91	10/10/12	8/01/13	91	6	2	982		979	3			42		41	1		
7415	74	9/10/12	591	9/10/12	15/10/13	371	12	4	619	2	164	10	443		64	1	54	4	6	
7416-1	90	9/10/12	304	9/10/12	7/10/13	363	18	4	1,212	9	773	19	411		77	3	64	4	8	
52642	89	9/10/12	156	9/10/12	14/03/13	156	10	3	41,497		346	321	40830		101		4	3	94	
33181	81	11/01/13	497	11/01/13	4/03/13	52	11	1	10,868					10868	43					43
7417-2	69	11/01/13	497	11/01/13	27/05/14	501	9	4	87		3	34	5	45	35		2	11	2	20
33185	70	11/01/13	497	11/01/13	5/07/14	540	13	4	67,040	14	16	4	36299	30707	240	2	1	1	36	159
33186	86	11/01/13	497	11/01/13	20/04/14	464	10	4	13,219	247		2	10845	2125	190	6		1	30	155
7416-2	32	23/05/14	61	23/05/14	22/07/14	60	1	1	5,928				5,928		61				61	
Total									521,544	4,772	22,629	8,058	353,679	132,406						

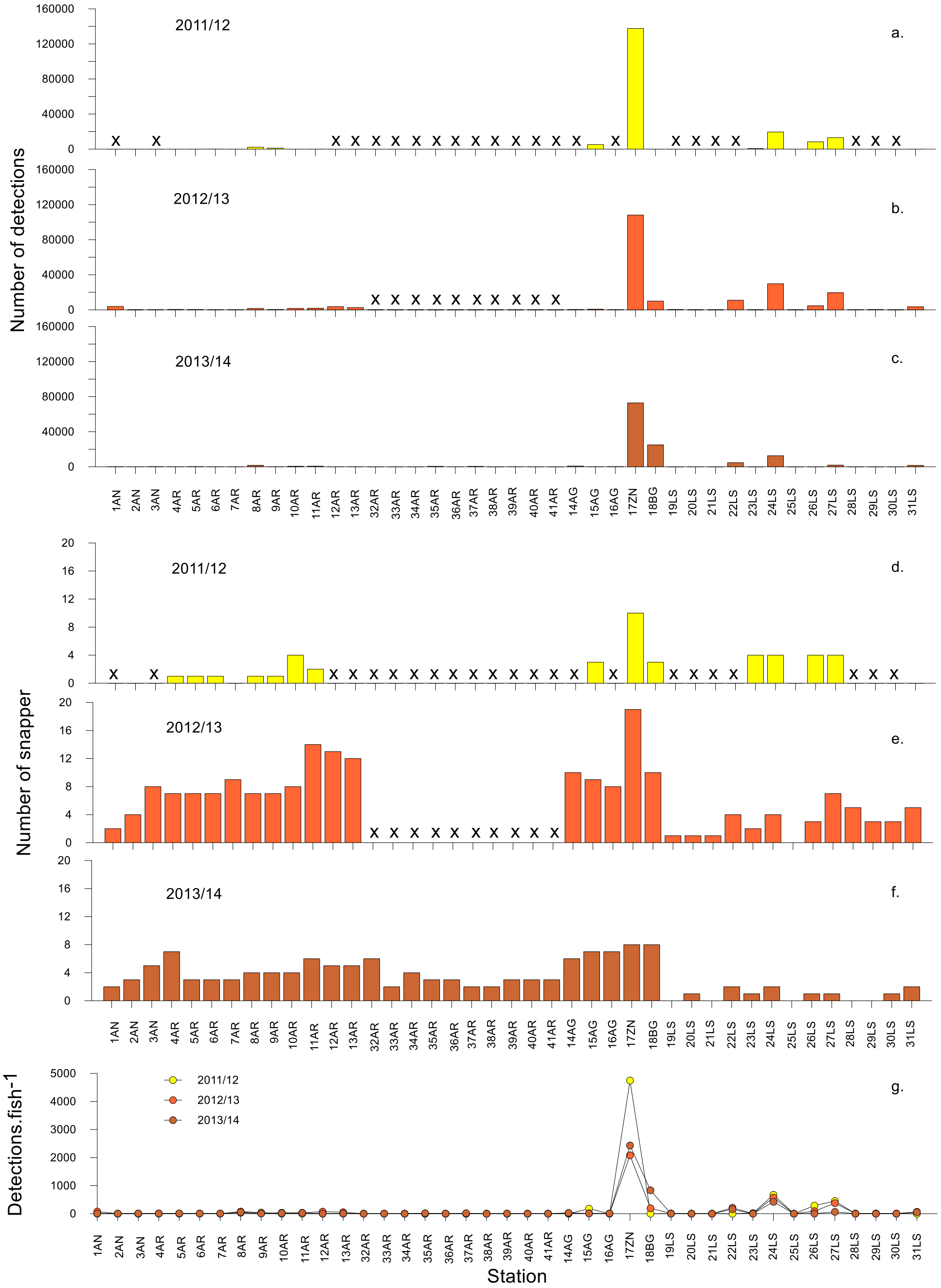

Fig. A11.3. Summary of spatial results of the acoustic telemetry study in NGSV at the scale of station. a, b, c. detections recorded per year at each station; d, e, f. number of snapper detected per year at each station; g. number of detections per viable fish per station. ‘x’ indicates that station was not monitored in that year.

12. REGIONAL VARIATION IN DEMOGRAPHY AND POPULATION DYNAMICS

Anthony Fowler

12.1 Introduction

Throughout Australasia, large populations of Snapper tend to be located near significant nursery areas. This is apparent in Cockburn Sound and Shark Bay in Western Australia, Moreton Bay in Queensland and the Hauraki Gulf in New Zealand. For the south eastern part of Australia, the regions that support primary nursery areas as well as high adult abundances and important fisheries of Snapper (*Chrysophrys auratus*) are located in Port Phillip Bay (PPB) in Victoria (Hamer et al. 2011) and for South Australia in the northern part of Spencer Gulf and possibly also Northern Gulf St. Vincent (Chapter 6, Fowler 2016, Fowler et al. 2017).

Throughout the 2000s, for each of South Australia and Victoria, there has been a high level of connectivity between adjacent regional populations as large numbers of sub-adult and adult fish migrated from the primary nursery areas to adjacent regional populations regions over distances of up to hundreds of km (Chapter 10, Hamer et al. 2011, Fowler et al. 2017). Recruitment to the primary nursery areas is characterised by high inter-annual variation (Chapter 6, Fowler and Jennings 2003, Hamer and Jenkins 2004). As such, the rates of emigration of Snapper from natal regions and their dispersion to other regions also varies from year-to-year, depending on year class strength. This represents a form of density dependent range expansion into regions that would otherwise depend on local recruitment (Hamer et al. 2011, Fowler et al. 2017). The lag between the timing of 0+ recruitment and subsequent dispersion to adjacent regional populations would likely depend on the distance between them and relative year class strength.

The current model of stock structure for South Australian Snapper involves three stocks, each of which is thought to depend on a primary nursery area (Fowler 2016, Fowler et al. 2017). The Spencer Gulf/West Coast Stock involves the regional populations of the northern and southern parts of Spencer Gulf (NSG, SSG) and the west coast of Eyre Peninsula (WC) (Fig. 12.1). For this stock the major nursery area is located in NSG (Chapter 6). The Snapper population in the south-east of South Australia (SE Region) is part of the Western Victorian Stock that is supplemented by emigration from PPB, Victoria (Hamer et al. 2011, Fowler et al. 2017). The Gulf St. Vincent Stock involves the regional populations of northern and southern Gulf St. Vincent (NGSV, SGSV). As yet, the location of the primary nursery area for this stock remains unresolved (Chapter 6).

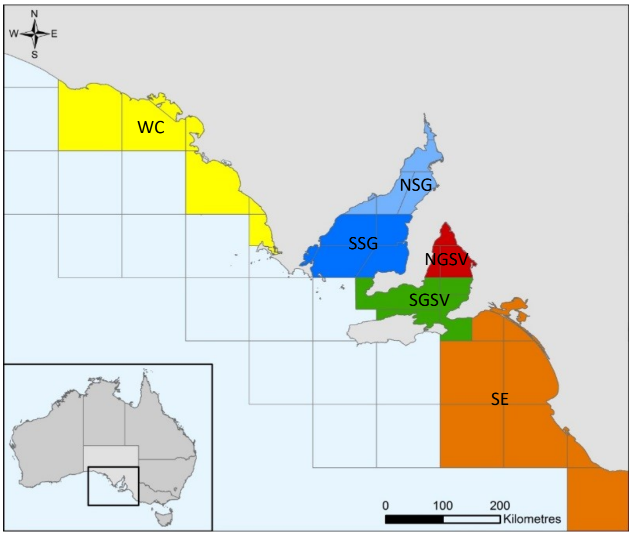

Fig. 12.1 Map of South Australian coastal waters showing the six regional populations that constitute the Spencer Gulf/West Coast Stock (NSG, SSG, WC), the Gulf St. Vincent Stock (NGSV, SGSV) and the SE Region that is part of the Western Victorian Stock.

Over the past 20 years there have been significant changes in the spatial structure of South Australia's Snapper fishery. Historically, the Spencer Gulf/West Coast Stock made the dominant contribution to the State's catches (Fig. 12.2) (Fowler et al. 2020). Up to the early 2000s, the catches were dominated by those from NSG, which at the time was the most productive regional Snapper fishery in Australia (Fowler et al. 2010). Whilst from 2005 to 2008, SSG produced the highest regional catches, from 2007 onwards, the catches from both NSG and SSG declined considerably. Yet, around the same time, the catches and catch rates in Gulf St. Vincent increased exponentially to unprecedented levels before they also declined through the latter 2000s. The increase mostly occurred in NGSV with that in SGSV being considerably less significant. For the SE Region between 2004 and 2010, the fishery catches increased exponentially, but then declined to a very low level by 2016. The different trends in fishery statistics for the three stocks are indicative of contrasting trends in population dynamics. They indicate that the timing of the variation in recruitment and inter-regional movement must have differed amongst the three stocks. For the future management of South Australia's Snapper fisheries, it would be highly beneficial to understand the timing of these demographic processes as they occurred for the different stocks and the extent to which they were independent or inter-connected. This was the focus of this chapter. The approach used was to describe the temporal variation in fishable biomass and to relate this to the timing of variable recruitment and large-scale, inter-regional migration of fish.

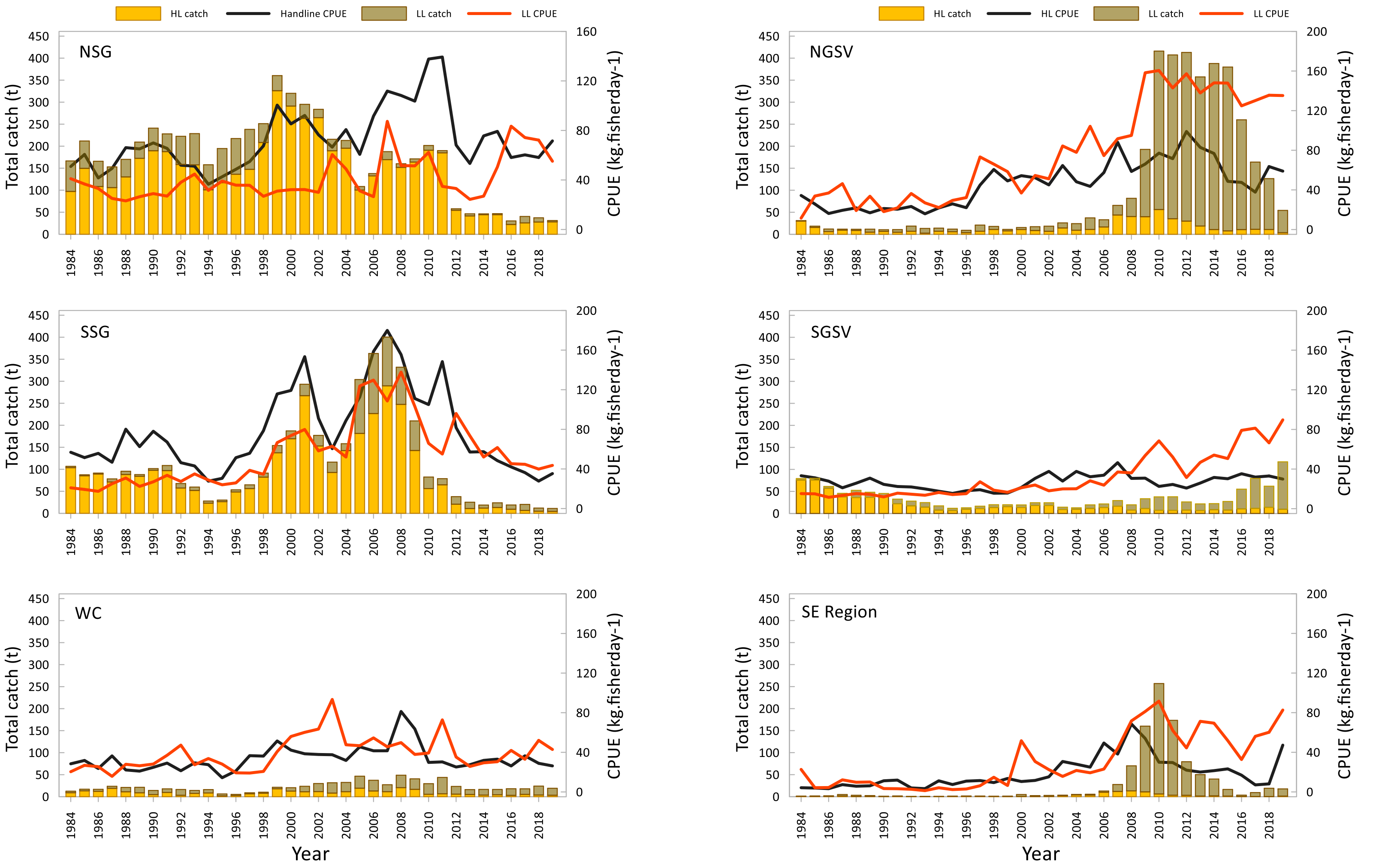

Fig. 12.2 Annual estimates of commercial fishery statistics at the regional spatial scale for the populations of the Spencer Gulf/West Coast Stock (NSG, SSG, WC), the Gulf St. Vincent Stock (NGSV, SGSV) and the SE Region that is part of the Western Victorian Stock. Data show the annual estimates of handline and longline catches and CPUE.

12.2 Materials and methods

In this chapter, several independent datasets that have been collected over the past 20 years or so, were interpreted in the context of population dynamics. Although the recent focus in managing South Australia's Snapper fishery has been directed at the scale of stock (Fowler et al. 2020), there is evidence that demographic processes differ among the regional populations that comprise these stocks (Fowler et al. 2013, 2016). As such, while the focus here was ultimately at the scale of stock, some datasets relating to processes were considered at the regional spatial scale. These datasets included the commercial fishery statistics that were summarised in Fig. 12.2. Secondly, population age structures were considered in the context of the variation in fishery catches as well as output from the SnapEst computer fishery model. The development of the regional age structures was summarised in Chapter 9. Then, there were the time series of output parameters from the SnapEst model for each of the Spencer Gulf/West Coast Stock, Gulf St. Vincent Stock and the SE Region, i.e., annual estimates of biomass and recruitment (Fowler et al. 2020). Furthermore, outcomes from historic otolith chemistry studies were considered that had focussed on population processes at the regional spatial scale (Fowler 2016, Fowler et al. 2004, 2005, 2017). These studies had targeted the strong year classes for those regions, addressing questions about the natal origins of the strong year classes and the timing of dispersion of fish amongst regions (Chapter 10).

12.2.1 SnapEst computer fishery model

The SnapEst computer fishery model integrates complex datasets to generate time-series of output parameters that relate to important demographic trends. It is a dynamic, spatial, age- and length-structured model that integrates several datasets to estimate time series of output parameters (McGarvey and Feenstra 2004). The input parameters include: time series of commercial fishery statistics (Fig. 12.2); and the annual, regional population size and age structures that were summarised in Chapter 9. In recent assessments the model inputs have also included estimates of spawning biomass determined using DEPM (Fowler et al. 2020, Drew et al. 2022). SnapEst interprets these input datasets in terms of population processes, ultimately producing maximum likelihood estimates of the four biological performance indicators of: i) fishable biomass; ii) numbers of recruits; iii) harvest fraction; and iv) egg production. For stock assessments, these provide biological performance indicators that are assessed against reference points, to indicate fishery status (PIRSA 2013). From a biological perspective, the SnapEst model simulates the population dynamics for the different stocks. The resulting time series of output parameters provide insight into these population dynamics and the processes that drive them.

When the SnapEst model was updated and run for the stock assessment undertaken in 2020 (Fowler et al. 2020), it incorporated fishery statistics up to 2019 (Fig. 12.2), and the regional size and age structures that were generated up to and including 2020 (Appendix Chapter 9 Figs. A9.1-

A9.5). The model was run at the spatial scale of 'stock', generating the annual time series of fishable biomass and recruitment that were considered here.

12.2.2 Otolith chemistry studies

There have been two otolith chemistry studies undertaken for Snapper in South Australia that have considered otoliths from regional populations (Chapter 10, Appendices 10.6). Both studies addressed issues around the natal origins of fish and the connectivity among regions by movement of large numbers of fish. The first study, done during the early 2000s, considered otoliths from fish from six regional populations (NSG, SSG, WC, NGSV, SSG, SE Region). These were nine-year old fish from the strong 1991-year class that were sampled in 2000 (Fowler et al. 2004, 2005). Elemental profiles across the otoliths were generated by laser ablation inductively coupled plasma mass spectrometry (ICPMS) from which were calculated age-related annual estimates of Ba and Sr concentrations (Appendix 10.6.1). The second otolith chemistry study had similar objectives and used a similar approach but was done at a larger scale (Chapter 10, Fowler 2016, Fowler et al. 2017). Fish from four strong year classes i.e., 1991, 1997, 2001 and 2004 were considered (Chapter 9, Appendix 9.6). Snapper otoliths from five South Australian regions (NSG, SSG, NGSV, SGSV, SE) and from Port Phillip Bay (PPB), Victoria were considered. Transverse sections of the otoliths were sampled using laser ablation ICPMS across the chronological structure of the otoliths. For each year class, the annual estimates of concentrations of Ba/Ca, Sr/Ca, Mn/Ca and Mg/Ca were compared amongst regions (Appendix 10.6.2).

12.3 Results

12.3.1 Spencer Gulf/ West Coast Stock

This stock involves three regional populations (Fig. 12.1). For NSG, from 1984 to 2019, total commercial catches varied cyclically showing several modes with peaks in 1990, 1999 and 2010 (Fig. 12.2). The total catches were relatively high until 2011, declined considerably in 2012 and subsequently remained low. The catch rates showed similar cyclical variation. Such fishery statistics are indicative of variation in biomass. The population age structures involved three strong year classes that recruited through the 1990s, i.e., the 1991, 1997 and 1999-year classes (Fig. 12.3, Chapter 9 Appendix Fig. A9.1). There were no comparable strong year classes that recruited to this region throughout the 2000s.

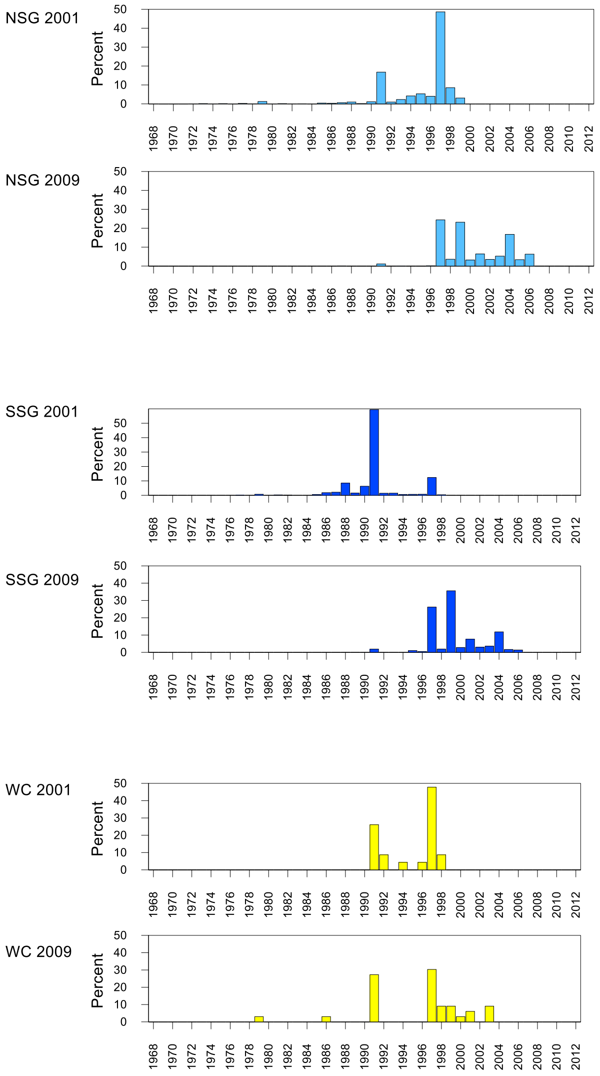

Fig. 12.3. Population age structures for NSG, SSG, and the WC in 2001 and 2009. For the first two regions, age structures for other years from 2000 are available in Chapter 9, Appendix Figs. A9.1 and A9.2).

For SSG, there were relatively low catches and catch rates particularly during the mid-1990s, as well as during the 1980s (Fig. 12.2). These increased considerably during the late 1990s and again through the mid-2000s. There were two obvious modes in the fishery statistics that occurred through the first decade of the 2000s. Then, between 2007 and 2019, catches and catch rates declined considerably. The age structures involved three strong year classes that dominated the populations through the 1990s and 2000s until 2014, i.e., the 1991, 1997 and 1999-year classes (Fig. 12.3, Chapter 9 Appendix Fig. A9.1).

For the populations on the WC, the annual catches and catch rates have been considerably lower than those from NSG and SSG (Fig. 12.2). The catches and catch rates increased to relatively high levels in 2005 from their lowest levels in 1995 and 1996. From 2011, they declined again to relatively low levels. Between 2000 and 2012, the 1991 and 1997-year classes were dominant and persistent year classes. These were two classes that dominated in NSG and SSG, through the same period (Fig. 12.3).

In 2020, the SnapEst model for the Spencer Gulf/West Coast Stock integrated the commercial fishery statistics and population age structures from NSG, SSG and the WC, generating time series of estimates of biomass and annual recruitment for the whole stock (Fowler et al. 2020). The resulting estimates of biomass for between 1984 and 2020 ranged from 468 to 5,351 t (Fig. 12.4a). Up to 1993 they declined, before increasing again in two phases; first to 1998, and subsequently to a record peak in 2005. From then, there was a continuous, long-term decline down to the lowest level in 2020. The temporal trends in estimated biomass related to variation in recruitment rates. Whilst the declining biomass until 1993 reflected poor recruitment throughout the 1980s, the following recovery related to the recruitment of the 1991-year class, which produced many times the numbers of recruits than most other years (Fig. 12.4a). Further increases in biomass up to 2005 reflected the influence of two further strong year classes in the 1990s, i.e., in 1997 and 1999. From 2005, the declining biomass reflected poor recruitment throughout the 2000s, i.e., a long period without recruitment of any strong year classes. The age structures and recruitment time series indicate that through the 35-year period from 1983 to 2017 there were only three particularly strong recruitment year classes.

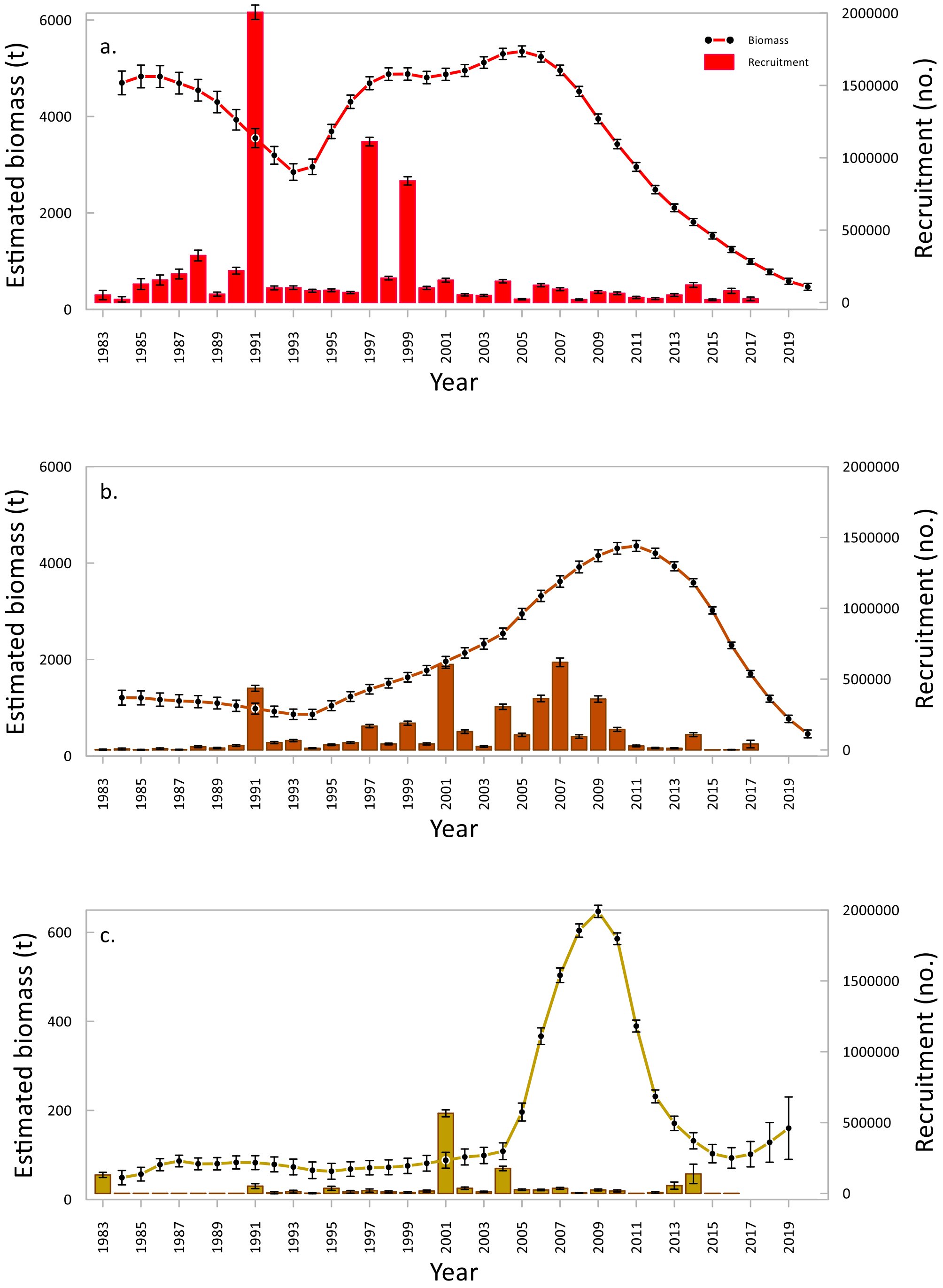

Fig. 12.4. Time series of estimates of biomass and annual recruitment rates from the SnapEst model (Fowler et al. 2020). a. for the Spencer Gulf/West Coast Stock; b. the Gulf St. Vincent Stock; c. the SE Region that is part of the Western Victorian Stock.

12.3.2 Gulf St. Vincent Stock

The Gulf St. Vincent Stock involves two regional populations, i.e., NGSV and SGSV (Fig. 12.1). From the 1980s to the 2000s, the former region characteristically produced both low catches and catch rates (Fig. 12.2). However, from 2004 to 2010, these both increased exponentially, culminating in record levels for the period from 2010 to 2015. They strongly indicated a substantial increase in biomass through the 2000s. The age structures included numerous strong year classes that had recruited in 1991, 1997, 1999, 2001, 2004, 2007 and 2009 (Fig. 12.5, Chapter 9 Appendix Fig. 9.3).

The regional fishery in SGSV is characterised by relatively low catches. Although high catches had been taken through the 1980s, they declined down to 1995 (Fig. 12.2). From then until 2011, the catches and catch rates increased slowly. In the latter 2000s, there were considerable increases in catches and catch rates. From 2000 to 2011, the fishery catches were dominated by the 1991 and then the 2001 and 2004-year classes (Fig. 12.5, Chapter 9 Appendix Fig. 9.4). From 2012, the 2006, 2007 and 2009-year classes became dominant.

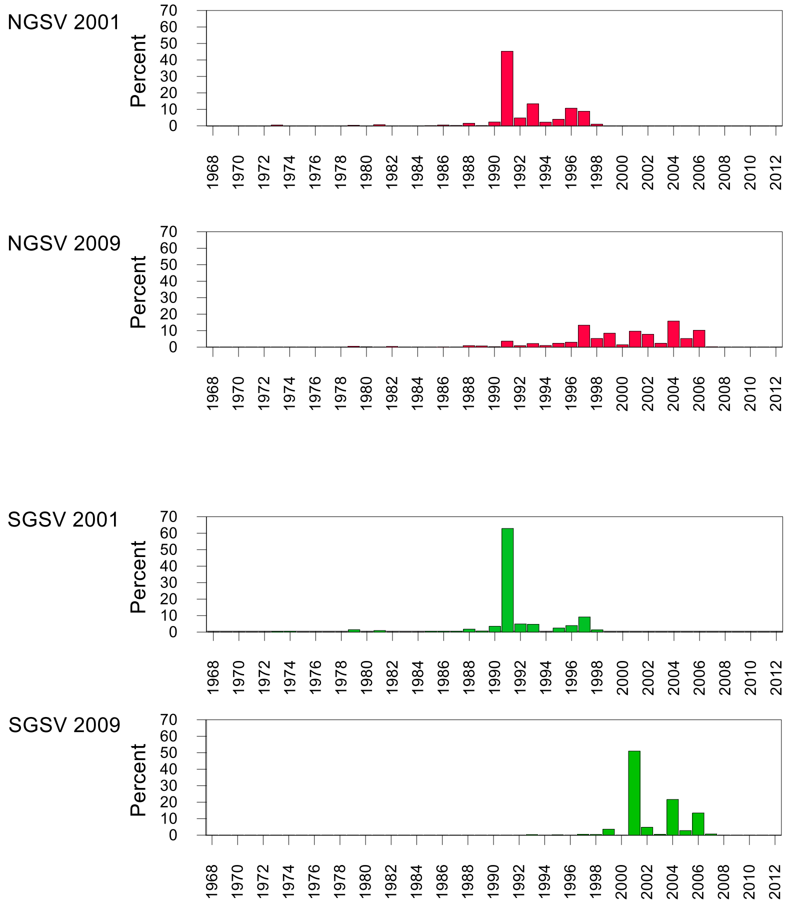

Fig. 12.5. Population age structures for NGSV and SGSV in 2001 and 2009. Age structures for other years are available in Chapter 9, Appendix Figs. A9.3 and A9.4.

Estimates of biomass for the Gulf St. Vincent Stock from the SnapEst model ranged over approximately an order of magnitude from 457 to 4,355 t. In the early 1980s, they were relatively low and continued to decline until 1994 (Fig. 12.4b). They then increased relatively slowly until 2004 after which the rate of increase accelerated to the highest level in 2011. From then until 2020, biomass fell considerably to its lowest level. The trends in biomass between 1984 and 2020 reflected the temporal variation in recruitment rates. The 1991-year class was relatively strong, as were the 1997 and 1999-year classes. The substantial increase in biomass that occurred throughout the 2000s related to the series of strong year classes that recruited in 2001, 2004, 2006, 2007 and 2009. It appears that those in 2014 and 2017 were also relatively strong (Fig. 12.4b).

12.3.3 South East Region

The SE Region of South Australia has generally produced only incidental catches of Snapper at low catch rates. However, from 2006 to 2010, there was an exponential increase that culminated in record commercial catches associated with a substantial increase in longline CPUE (Fig. 12.2). Since then, the annual catches have declined back to a low level. The increases in catches and catch rates related to a substantial increase in biomass. The annual age structures from 2008 to 2014 were dominated by the strong 2001 and 2004-year classes, which accounted for ~50-90% of the high annual commercial catches (Fig. 12.6, Chapter 9 Appendix Fig. A9.5). In 2000, when the fishery catches from the SE Region were quite low, the ages of 77 fish that were accessed through market sampling, were dominated by the 1991-year class (Fig. 12.6),

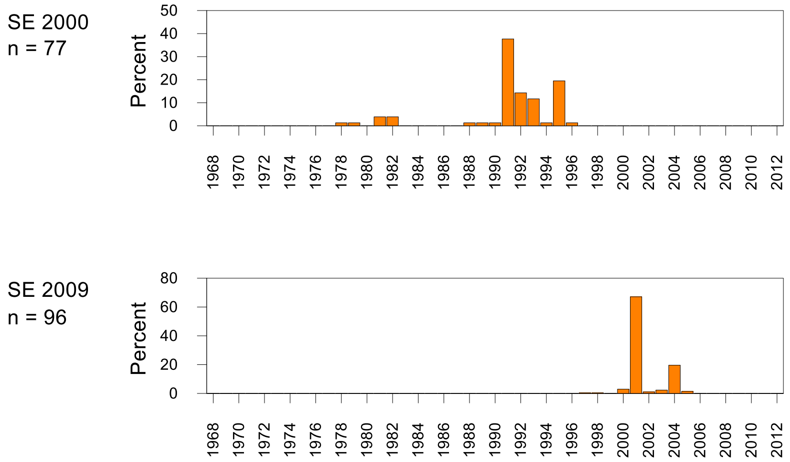

Fig. 12.6. Population age structures for the SE Region in 2001 and 2009. Age structures for other years are available in Chapter 9, Appendix Figs. A9.5.

The estimates of biomass from the SnapEst model for this regional population were relatively low until 2004 (Fig. 12.4c). After that year, there was a substantial increase until 2009, after which there was a considerable decline to 2012, and then further slower decline until 2016. Subsequently, there has been a marginal increase in biomass to 2019. The low biomass levels to 2004, reflect low incidental recruitment throughout the 1980s and 1990s. The considerable increase in biomass reflected the influence of two strong year classes; the first and strongest recruited as 0+ fish in 2001, after which the population was further augmented by the 2004-year class.

12.4 Discussion

The time series of annual estimates of biomass from the SnapEst model show different temporal patterns amongst the Spencer Gulf/West Coast Stock, Gulf St. Vincent Stock, and the population of the SE Region. The Spencer Gulf/West Coast Stock supported the highest biomass through the 1980s, 1990s and early 2000s during which the biomass of the Gulf St. Vincent Stock was relatively low. However, around 2005 to 2010, there was a significant change whereby the biomass in Spencer Gulf/West Coast Stock decreased considerably whilst that for the Gulf St. Vincent Stock increased exponentially. At the same time, for the SE Region, there was a considerable episodic increase followed only a few years later by a significant decline.

These very different trends reflected the temporal patterns of recruitment into the different stocks. The two South Australian stocks involve several regional populations, whilst the SE Region is the western-most component of the Western Victorian Stock. The time series of biomass and recruitment were integrations of the demographic processes that occurred at the regional scale. In the text below, each region is considered, identifying the timing and scale of the demographic processes that accounted for the variations in fishery productivity and stock status that are now apparent for the past 20 years or so (Fowler et al. 2020).

12.4.1 Spencer Gulf/ West Coast Stock

Northern Spencer Gulf

This region made the dominant regional contribution to South Australia’s commercial catches until around 2005, which remained relatively high until 2011, before declining from 2012 onwards to very low levels. This is reflected in the decline in biomass estimates for the Spencer Gulf/West Coast Stock from the SnapEst model. The high levels of biomass through the 1990s and the first decade of the 2000s related to three strong year classes that dominated the fishery catches until 2015. The most exceptional one recruited in 1991, which drove the recovery in biomass through the mid-late 1990s. The two further strong year classes in each of 1997 and 1999 made further contributions to the increasing biomass. In contrast, the declining biomass from 2005 onwards was related to relatively poor recruitment to NSG after 1999. To understand the population dynamics of this regional population, it is important to know the natal origins of the three strong year classes.

NSG is a region that supports an important nursery area for recruitment of 0+ Snapper. This is evident from recruitment surveys and from surveys of by-catch from prawn trawling throughout the gulf (Chapter 6, Fowler and Jennings 2003). The region includes areas where there is preferred habitat into which the post-larvae undergo settlement to become juvenile fish. NSG is now recognised as a primary nursery area (Fowler et al. 2017), which has similar significance to that of PPB, Victoria, for the Western Victorian Stock (Hamer et al. 2011).

The chemistry of the otoliths from adult Snapper from NSG had elemental signatures that were characteristic for the region (Appendix 10.6). They typically had very low concentrations of Ba, reflecting low ambient levels. Furthermore, the otoliths also had low levels of Mn across their chronological structures compared with fish that had originated in PPB (see below). The low levels of Ba across the otoliths from the 1991, 1997, 2001 and 2004-year classes are consistent with these fish having originated in and subsequently having spent all or most of their lives in this region. On this basis, it is proposed that the population in NSG is self-sustaining and unlikely to have received recruitment through immigration from other regions, including PPB (Fowler et al. 2017).

Southern Spencer Gulf

For this region, the trends in commercial fishery statistics suggest that biomass increased through the late 1990s and from 2003 to 2007, increases that were encapsulated in the trends in estimated biomass for the Spencer Gulf/West Coast Stock from the SnapEst model. The increases reflected the influences of three strong year classes i.e., those that had recruited in 1991, 1997 and 1999 that dominated the regional age structures until 2015. These were the same year classes that drove the population dynamics in NSG. For SSG, the issue with respect to the factors driving the population dynamics is - from where did these fish originate?

The characteristics of otoliths from the different year classes showed considerable variation across their chronological structure. The first few increments generally had low levels of Ba, Sr and Mn. In this regard, there were obvious differences compared with the otoliths from PPB. This provides no evidence that fish from the Western Victorian Stock penetrated into SSG. In contrast, the characteristics of the first few otolith increments were identical to those from NSG. Nevertheless, from the 3-4 increment onwards, the characteristics of the otoliths from the two regions diverged. Furthermore, few juvenile Snapper were captured in this region as by-catch from prawn trawling (Chapter 6). The parsimonious interpretation of these empirical results is – the strong year classes originated in NSG after which during their fourth year and onwards, large numbers of individuals migrated southward into SSG replenishing the population in this region (Fig. 12.7).

West Coast

For the Snapper populations of the WC, the annual commercial catches of Snapper have historically been considerably lower than those from NSG and SSG. Catches and catch rates increased to relatively high levels in 2005 from low levels in 1995 and 1996, suggesting that biomass increased throughout the latter 1990s and early 2000s. The age structures indicated two predominant and persistent year classes that had recruited in 1991 and 1997. These were two of the three that dominated in NSG and SSG throughout the same period. The characteristics of otoliths from 20 fish from the 1991-year class from the WC were considered in the first otolith chemistry study. For their profiles of Sr and Ba concentrations as well as increment widths, there were significant differences amongst otoliths from the WC and those from NSG and SSG. However, these differences were age-related. For the first two increments, the characteristics from all three regions were identical, but then diverged from the third increment onwards. For fish from the WC, the Ba concentrations increased considerably suggesting that for fish of this age onwards, numerous individuals were exposed to considerably higher ambient concentrations than those from NSG.

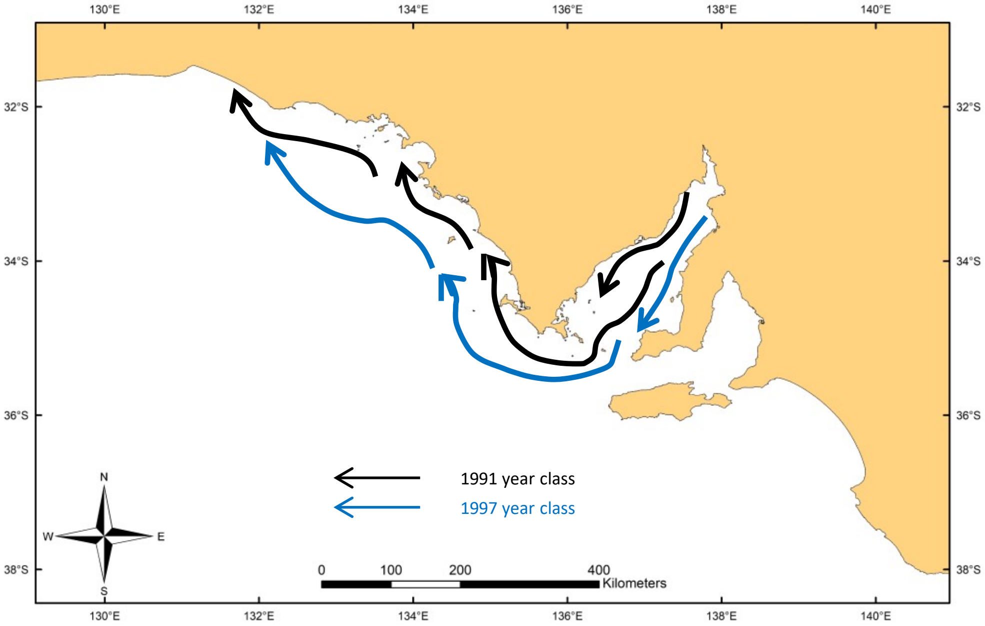

Fig. 12.7. Map of South Australian coastline and marine waters showing the likely dispersion of Snapper in the strong year classes of 1991 and 1997 from NSG to SSG and to the WC.

In combination, the age structures and elemental concentrations are consistent with individuals of the 1991-year class that were taken on the WC in 2000 having originated in NSG and having moved down through Spencer Gulf and into the oceanic waters of the WC and up to Streaky Bay, Denial Bay and even to Fowlers Bay (Fig. 12.7). The higher Ba content in the otoliths during the 3rd and 4th years is consistent with the movement of fish into oceanic waters. The strong 1997-year class in the three regions is consistent with the same processes of migration from NSG being responsible for fish reaching the WC. This proposed migration of fish to the WC significantly increases the spatial scale of dispersion of fish in the strong year classes that recruit to NSG (Fig. 12.7).

12.4.2 South East Region

The SE Region of South Australia has generally produced only incidental catches of Snapper at low catch rates. However, the exponential increases that occurred during the mid-2000s indicate a substantial episodic increase in biomass. This increase relates to the strong 2001 and 2004-year classes. As there is a lack of suitable nursery areas for Snapper in the SE Region, the primary questions about the population dynamics for this region were – where did fish in the strong 2001 and 2004-year classes originate and when did they arrive? These were addressed in the first and second otolith chemistry studies.

Fish from the 2001-year class from the SE Region had high elemental concentrations as well as ontogenetic trends in the first-formed annual increments that were similar to those from PPB. This suggests that the fish from both regions had a common origin and had occupied the same environment for several years from birth. It is most likely that the fish sampled from SE Region had originated in PPB. The latter primary nursery area for Snapper has high ambient levels of Ba that results in high concentrations in their otoliths (Hamer et al. 2006, 2011). Beyond the 3-4 increment, the ontogenetic trajectories in the otoliths from the SE Region and PPB diverged. This suggests that the timing of departure from PPB and movement to the SE Region commenced around three to four years of age.

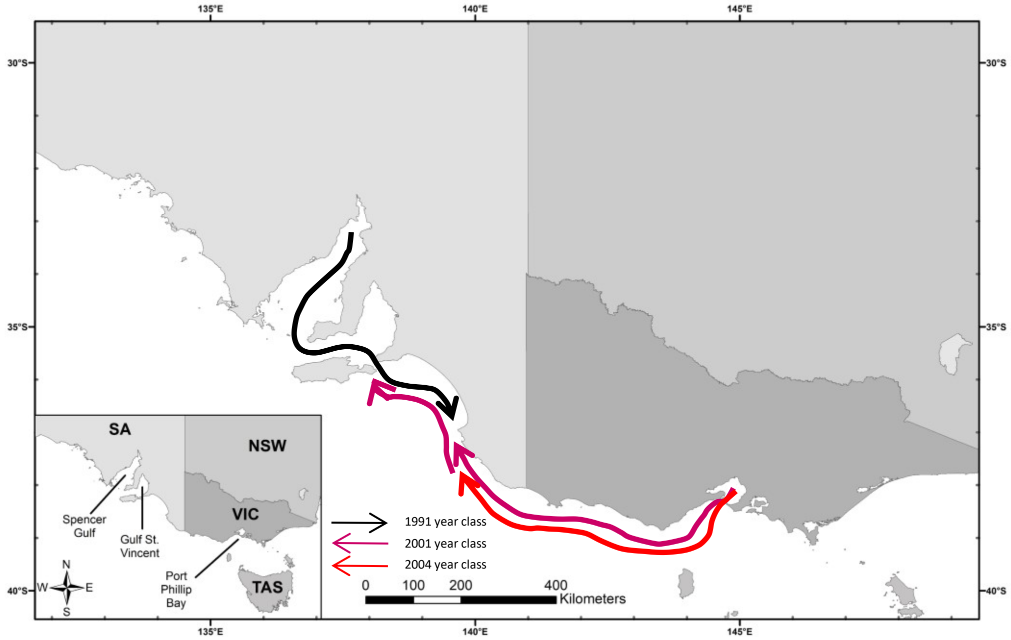

Fig. 12.8. Map of part of the southern Australian coastline and marine waters showing the likely dispersion of Snapper for the strong year classes of 1991, 2001 and 2004 to the SE region of South Australia.

For the 2004-year class, the otolith chemistry results were similar to those for the 2001-year class, suggesting that these migrants to the SE Region had also originated in PPB. This consistency between year classes strongly suggests that the population dynamics and productivity of the episodic fishery in the SE Region relate to recruitment to PPB, followed by mass emigration of sub-adult/adult Snapper from the bay and their movement over 600 km to the SE Region over a period of 3-5 years (Fig. 12.8). It appears that the exceptional strength of the 2001 and 2004-year classes in PPB is likely to have caused greater density dependent migration or ‘spill over’ into South Australian waters than had occurred historically. Such ‘spill over’ ultimately drove up the abundances and biomass in the region to the extent that the Snapper fishery flourished for about five years. It appears that there was not further significant augmentation of the population by migration of further strong year classes from PPB. Until recently there has been limited opportunity for significant recruitment to the SE Region, as until 2018, no recruitment year class to PPB has been as strong as the 2001 and 2004-year classes (Fowler et al. 2020).

The ephemeral nature of migration to the SE Region from PPB is demonstrated by the analyses of otoliths from fish for the 1991-year class that were sampled in 2000 (Fowler et al. 2004). Although in 2000 the fishery catches and estimated biomass for the SE Region were relatively low, it was still evident that the population was dominated by the 1991-year class. Furthermore, their otoliths showed considerable age-related variation (Fowler et al. 2004). The first few increments had extremely low levels of Ba, which subsequently increased and became more variable from the third increment onwards. Such low Ba levels indicate that these fish had not originated from PPB. Rather, the characteristics of the first four increments were similar to those of the otoliths from the South Australian gulfs. The strength of the 1991-year class for NSG and similarity in otolith characteristics for the first four increments suggest that these fish had originated in NSG and had eventually dispersed to the SE Region (Fig. 12.8).

For the SE Region, the empirical results with respect to fishery catches, estimated biomass, population age structures and retrospective analysis of the otolith characteristics suggest that the ephemeral nature of the population and fishery relate to it being sustained by migration from either the east or west, over distances of hundreds of km. The rates of such migration are density dependent and relate to the relative recruitment rates into the different nursery areas and subsequent spill-over in numbers and range expansion associated with such strong year classes.

12.4.3 Gulf St. Vincent Stock

Southern Gulf St. Vincent

Since 1984, the fishery catches and catch rates for Snapper from SGSV have generally been low relative to those from other gulf regions. Whilst throughout the 2000s the increasing catches and catch rates suggest the likelihood that biomass had increased, the relative contribution to the overall biomass of the Gulf St. Vincent Stock is likely to have been relatively minor. From 2000 to 2011, the fishery catches from this regional population were dominated by the 1991 and then the 2001 and 2004-year classes. There is no known nursery area for Snapper in this region. So, the question is - from where did the fish in these strong year classes originate and when did they arrive?

For the 2001-year class in SGSV, the ontogenetic trends and elemental concentrations in the first formed annual increments in the otoliths were similar to those from PPB and the SE Region. As for the latter region, this suggests that these fish had originated in PPB and had completed a significant westward journey of approximately 800 km from the nursery area (Fig. 12.9). In contrast, the otoliths from the 2004-year class had different otolith chemistry from those from PPB and the SE Region but were similar to those from NSG and NGSV. This indicates a different geographic source for these fish. Through the 2000s, there were no strong year classes that recruited to NSG. By this time, biomass had increased in Gulf St. Vincent, and the 2004-year class was relatively strong in NGSV. This suggests that the strong year class in SGSV had likely originated from local recruitment into the Gulf St. Vincent Stock, possibly from NGSV (Fig. 12.9).

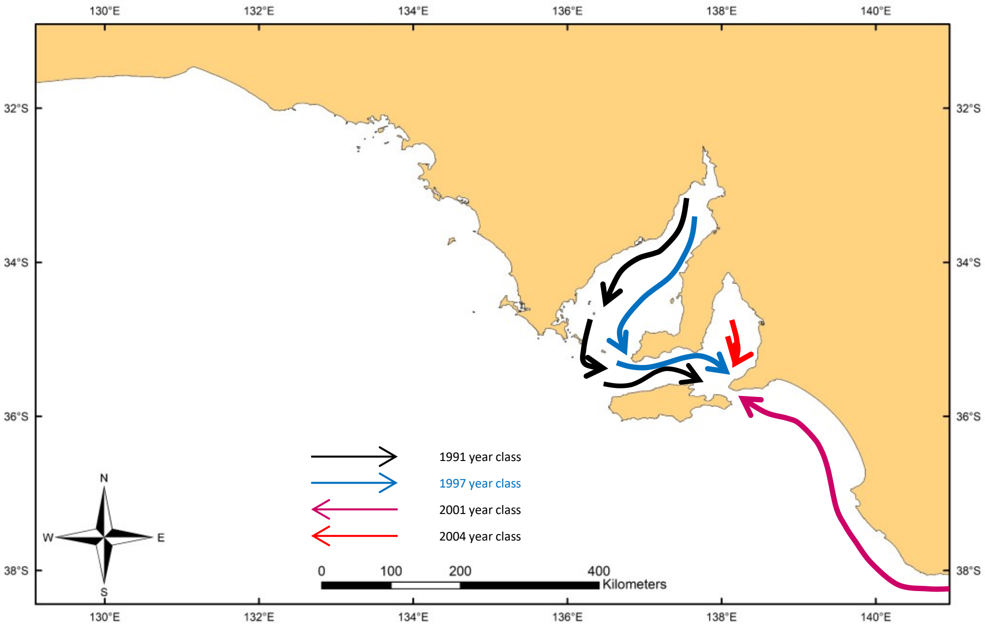

Fig. 12.9. Map of South Australian coastline and marine waters showing the likely dispersion of Snapper to SGSV for the 1991 and 1997-year classes from NSG, the 2001-year class from PPB via the SE Region and the 2004-year class from local recruitment in GSV.

The otolith chemistry results for the 1991 and 1997-year classes in SGSV also excluded PPB as the source of recruits. During the 1990s, the biomass in NSG was considerably higher than in NGSV, relating to the strength of the 1991 and 1997-year classes. Given the likelihood that immigrants of these year classes were dispersing from NSG throughout SSG and the WC, it is likely that some migrated to SGSV through SSG and Investigator Strait (Fig. 12.9).

Northern Gulf St. Vincent

The fishery statistics for NGSV indicate a substantial increase in biomass through the first decade of the 2000s. This increase dominated the estimates of biomass for the Gulf St. Vincent Stock by the SnapEst model. The increase in biomass was related to numerous strong year classes i.e., the 1991, 1997, 1999, 2001 2004, 2006, 2007 and 2009-year classes. The overriding issue with respect to the population dynamics for this region relates to how the biomass built up so quickly through the 2000s. It is now apparent from the discussion above that PPB, Victoria and NSG are primary nursery areas in south-eastern Australia, and emigration from these is an important source of replenishment for other regional populations. As such, there is the question as to whether numerous strong year classes in NGSV built up through migration from either of these nursery areas or through local reproduction and recruitment.

The otolith chemistry results for individuals from NGSV for the four strong year classes of 1991, 1997, 2001 and 2004 demonstrated some consistencies in elemental concentrations across year classes. For all, there were clear consistent differences in elemental concentrations between those for NGSV and those from PPB and the SE Region. These data indicated that there had not been significant movement into NGSV of individuals that had originated in PPB, even from the strong 2001-year class from PPB that were evident in SGSV.

The remaining hypotheses about replenishment of this regional population are: the population was self-recruiting and abundances and biomass accumulated through local reproduction and recruitment over several years; or the population was replenished by dispersion from one or several strong year classes from NSG. Generally, the results from the otolith chemistry studies indicated similar age-related average elemental concentrations for fish from NSG and NGSV, with only subtle differences between regions for some elements and age classes. This general similarity is likely to relate to the comparable geography and similar environmental conditions of the two regions. As such, the estimates of average age-related elemental concentrations presented in Chapter 10 are difficult to interpret in terms of fish movement. However, the profiles of elemental concentrations for individual fish could be more useful. If Snapper had moved between NSG and NGSV, this should be evident in the chronological elemental concentrations as age-related changes in Ba concentrations, associated with movement from NSG, through SSG, Investigator Strait, and SGSV into NGSV. The otoliths from NGSV did display several types of profiles that are consistent with different life histories (Fowler et al. 2004). Several had low, flat profiles of Ba concentration, consistent with fish originating and remaining in NGSV throughout their lives. However, several other otoliths had elevated, age-related concentrations of Ba. These are more consistent with fish having moved into NGSV through southern waters. There were also several otoliths that had relatively high Ba concentrations in their first increment, suggesting origins in a southern environment with relatively high ambient Ba concentrations. This suggests that the 1991-year class in NGSV had three possible different origins: those fish that originated in NGSV and remained there; some that originated in NSG as part of the exceptional 1991-year class and eventually moved to NGSV during the dispersion of those fish throughout all regional South Australian waters; and fish that had originated in a southern region and eventually moved north into NGSV (Fig. 12.10).

The 1997-year class was a strong one in NSG. As such, it is possible that some of these fish dispersed from NSG to NGSV. In so doing, they would have added to the biomass in NGSV and contributed to the relative significance of this year class. Throughout the 2000s, there were no strong year classes that recruited to NSG, suggesting that further movement of large numbers of Snapper from NSG to NGSV was unlikely. It is suggested that the build-up in biomass for the Gulf St. Vincent Stock that occurred through the late 1990s provided sufficient spawning biomass for the population to become self-sustaining, and to generate the sequence of strong year classes that subsequently followed throughout the 2000s.

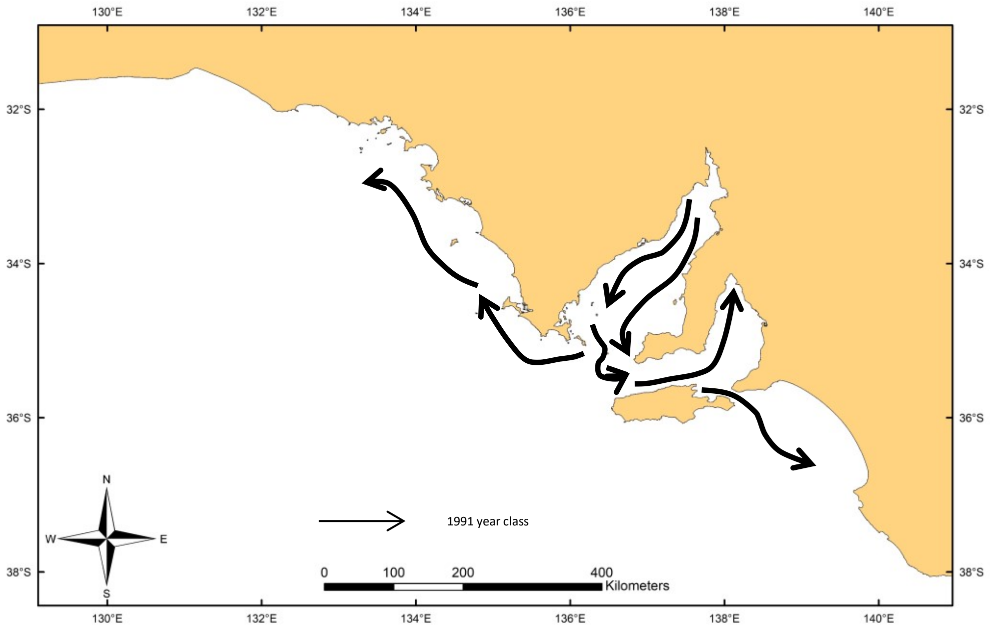

Fig. 12.10. Map of South Australian coastline and marine waters showing the proposed dispersion of the 1991-year class from the primary nursery area in NSG to all other SA regional coastal marine waters.

12.4.4 Conclusions

Over the past nearly 40 years, the three Snapper stocks that occur in or overlap with South Australia's marine coastal waters demonstrated considerable dynamics in their sizes, population characteristics and fishery productivity. These resulted in significant changes to the spatial structure of the State's fishery, i.e., changes over time in the relative contributions of the different stocks to the total annual catches. The focus in this chapter was to elucidate the specific demographic processes and their timing that drove such temporal variation. Several complex datasets were considered. Regional commercial fishery catches and catch rates were interpreted as indicators of population biomass. Also, regional population age structures were interpreted in terms of year class strength, successfully identifying strong recruitment years and periods of poor recruitment. These two datasets were integrated in SnapEst to provide stock-wide estimates of biomass and recruitment (Fowler et al. 2020). Furthermore, two otolith chemistry studies that considered otoliths from several strong year classes, quantified the elemental concentrations across their chronological structure, informing about the natal origins and timing of inter-regional movement.

The population dynamics were fundamentally driven by inter-annual variation in recruitment rates to the two primary nursery areas, i.e., NSG in South Australia and PPB in Victoria. The patterns of variation in recruitment rates differed between these nursery areas. For both NSG and PPB, the abundances and biomass of Snapper built up for several years following the recruitment of strong year classes. Then, this led to emigration of fish from these natal regions and their dispersion to adjacent regions over distances of a few hundred km up to approximately 1,000 km. This is likely a density dependent process that involved many thousands of fish.

For PPB, some of the strong 2001- and 2004-year classes emigrated from the bay and moved to and replenished the regional populations of western Victoria (Hamer et al. 2011). However, many such fish from both year classes moved even further to the west, reaching the SE Region in South Australia, replenishing the population in this region. This led to its episodic fishery. Some fish from the strong 2001-year class in PPB also moved as far west as SGSV, which is located approximately 800 km from the natal nursery area. The geographic locations of the SE Region and SGSV are particularly significant because, at different times, they have received migrants from both the primary nursery areas, i.e., during the 1990s from NSG and then during the 2000s from PPB.

For the other regional populations of South Australia, one of the most significant demographic processes of the past 30 years or so, was the recruitment of the 1991 year-class into NSG. In the following years there was significant emigration from this region and dispersion of fish throughout all the coastal marine waters of South Australia including SSG, WC, SGSV, NGSV and the SE Region. This immigration of the 1991 year-class and probably also the 1997 year-class to NGSV, was particularly significant. It is proposed that as a result of that immigration, a significant self-recruiting population was established whose biomass continued to build up through the 2000s, based on the production of a number of locally-produced, strong recruitment year classes. This led to the significant build-up in biomass and record fishery catches recorded in NGSV during the mid-2000s. This idea proposes the existence of one or several significant nursery areas in NGSV and/or SGSV, whose whereabouts, as yet remain unknown.

In November 2019, the fisheries for the Spencer Gulf/West Coast Stock and the Gulf St. Vincent Stock of Snapper were closed to fishing (Fowler et al. 2020, Drew et al. 2022). This was necessary as the stock status classifications for both stocks had been declining for several years. Based on the understanding of the processes that drove the dynamics of the regional populations, it is possible to retrospectively determine how both stocks ended up being classified as depleted. Throughout the 2000s, NSG received relatively poor recruitment. As such, there was only limited migration to and replenishment of populations in adjacent regions. Nevertheless, high fishery catches continued to be taken, first from NSG, then SSG. Thus, whilst the adult biomass in these regional populations were being reduced through fishing, they were not being sufficiently supplemented through the natural processes of reproduction, recruitment, and migration. This subsequently happened also for the regional populations in NGSV and SGSV. During the periods when the stock sizes were declining, there was insufficient timely information that the recruitment rates were consistently low. Furthermore, since Snapper is an aggregating species, it demonstrates ‘hyperstability’, i.e., high catches and catch rates can persist even when biomass is declining. This was the case for Snapper until the biomass of the various regional populations were much reduced.

12.4.5 Looking to the future

As evident from this report, there is now a good understanding of the demographic processes that drive the dynamics of the various regional populations, including inter-regional migration. Based on this, we need to consider what is required in the future to ensure that, once the South Australian Snapper stocks have recovered and the fisheries are reopened, that the same process of stock depletion does not recur. To achieve this, it will be necessary to have real-time understanding of how regional biomass is driven by recruitment. The importance of instigating annual monitoring of recruitment for the South Australian populations was clearly identified at the National Snapper Workshop in 2019 (Cartwright et al. 2020), in recognition of the significance of the long-term recruitment dataset that is now available for the Victorian Snapper populations (Hamer and Conron 2016). Such a monitoring program is being established in South Australia. In recent years there has been considerable effort invested through FRDC Project 2019/046, to determine the best method for sampling the 0+ age class. Furthermore, it is now evident that by-catch studies for prawn trawling can provide useful information on the abundances of the 1+ age class. Implementing sampling programs that independently focus on the 0+ and 1+ age classes will provide multiple indicators of relative year class strength, providing confidence in estimates of the input rates to the primary nursery area in NSG. For the Gulf St. Vincent Stock, understanding about recruitment is poor. The locations of the nursery areas are at present unknown. Also, until recently, the limited information on the temporal nature of recruitment has come from adult age structures, which means that there has been a delay of several years in the estimate of relative strength of each new year class. From FRDC Project 2019/046, there is some minimal information regarding the locations of the nursery areas. Continuing this work and implementing recruitment monitoring are important priorities for this stock, so that appropriate data on the timing and variation in recruitment can be considered.

It is evident that the temporal patterns in recruitment to the primary nurseries of NSG and PPB differ, reflecting different environmental drivers. The temporal variation in recruitment to PPB is related to the influence of the inflow of nutrients to the bay and the ensuing plankton dynamics (Murphy et al. 2012, 2013), but for NSG there is far less understanding about the physical and biological processes that led to generating the rare super year classes. Nevertheless, perhaps at present, in the context of the declining stocks, the greater concern is about the failure throughout the 2000s to generate a super year class. It was suggested earlier in this report that the general poor recruitment in Spencer Gulf throughout the 2000s, following the three strong year classes during the 1990s, might reflect an influence of climate change (Chapter 7). Increasing SSTs in Spencer Gulf may have either directly or indirectly affected the generation and/or survivorship of the eggs and larvae. Resolving this presents an important scientific challenge that has significant consequences for the likelihood and timing of stock recovery and the reopening of the fisheries. This is a focus of Theme 1 of the National Snapper Science Program.

Whilst there will be a clear focus on recruitment in the future, it will also be necessary to monitor the biomass of the Snapper populations. This will inform about how they respond to variable recruitment and fishery catches and provide the basis for controlling the regional total allowable catches, since future management of the Snapper fisheries will be based on fish quotas (Smart et al. 2022). Determining the best method for monitoring the biomass of the Snapper populations in the future is being addressed in Theme 2 of the National Snapper Science Program. For the adult populations, it will also be a priority to continue to monitor the population age structures. In the past, such data have provided invaluable insights into the regional populations informing about demographic processes. The continuation of such work will continue to inform about the timing and scale of the influence on populations of variable recruitment and inter-regional movement, as well as any changes in the age-based parameters. In so doing, the age structures will continue to be important input parameters to the SnapEst model for assessing the recovery of the stocks and informing about stock status. This will be fundamental to the process of assessment and decision-making for re-opening the fisheries of the Spencer Gulf/ West Coast Stock and the Gulf St. Vincent Stock. Protocols for monitoring population age structures have been well established in recent years (Drew et al. 2022).

The thoughts presented above regarding the scientific issues for the future are well represented in the plans for research in South Australia. Following the extension of the fishery closures in South Australia until 2026 that was the consequence of the most recent stock assessment (Drew et al. 2022), the South Australian State Government and the Fisheries Research and Development Corporation (FRDC) have collaborated to establish a significant support package and substantial science program towards recovering the stocks and reopening the fisheries. This has involved the establishment of a National Snapper Science Program, under three FRDC projects, for which the empirical work will be undertaken in South Australia but will have broader significance. The three themes of this program that will be undertaken in the next few years are aimed at improving our understanding of the population biology and ecological requirements of the species as well as improving the methods used for the collection of data that underpin and the processes involved in undertaking stock assessments.

12.5 References

Cartwright, I., McPhail, J., Knuckey, I., Smith, T., Rayns, N., Steer, M. (2020). National Snapper Workshop – Rebuilding our iconic Snapper stocks. Final report to FRDC (Project No. 2019/085). 58 pp.

Drew, M.J., Rogers, T.A., McGarvey, R., Feenstra, J., Matthews, D., Matthews, J., Earl, J., Smart, J., Noell, C., and Fowler, A.J. (2022). Snapper (*Chrysophrys auratus*) Stock Assessment Report 2022. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2007/000523-7. SARDI Research Report Series No. 1155. 178 pp.

Fowler, A.J., 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., Hall, K.C. (eds) (2004). Adult migration, population replenishment and geographic structure for snapper in SA. Final report to FRDC (Project No. 2002/001). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication Number RD04/0163. 152 pp.

Fowler, A.J., Gillanders, B.M., Hall, K.C. (2005). 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, R., Burch, P., Feenstra, J.E. Jackson, W.B. (2010). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-2, SARDI Research Report Series No. 473. Pp 109.

Fowler, A.J., McGarvey, R., Burch, P., Feenstra, J.E., Jackson, W.B., Lloyd, M. (2013). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, F2007/000523-3, SARDI Research Report Series No. 713. 103pp.

Fowler, A.J. (ed) (2016). The influence of fish movement on regional fishery production and stock structure for South Australia's snapper (*Chrysophrys auratus*) fishery. Final report to FRDC (Project No. 2012/020). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 181 pp.

Fowler, A.J., McGarvey. R., Carroll, J., Feenstra, J.E., Jackson, W.B., Lloyd, M.T. (2016). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-4. SARDI Research Report Series No. 930. 82pp.

Fowler, A.J. Hamer, P.J., Kemp, J. (2017). Age-related otolith chemistry profiles help resolve demographics and meta-population structure of a widely-dispersed, coastal fishery species. Fisheries Research 189: 77-94.

Fowler, A.J., Smart, J., McGarvey. R., Feenstra, J.E., Bailluel, F., Buss, J.J., Drew, M., Matthews, D., Matthews, J., Rogers, T. (2020). Snapper (*Chrysophrys auratus*) Fishery. Fishery Assessment Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences), Adelaide. F2007/000523-6. SARDI Research Report Series No. 1072. 111pp.

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

Hamer, P.A., Jenkins, G.P., Coutin, P. (2006). Barium variation in *Pagrus auratus* (Sparidae) otoliths: a potential indicator of migration between an embayment and ocean waters in south-eastern Australia. Estuarine, Coastal and Shelf Science. 68: 686-702.

Hamer, P.A., Acevedo, S., Jenkins, G.P., Newman, A. (2011). Connectivity of a large embayment and coastal fishery: spawning aggregations in one bay source local and broad-scale fishery replenishment. Journal of Fish Biology 78: 1090-1109.

Hamer, P.A., Conron, S. (2016). Snapper stock assessment 2016. Fisheries Victoria Science Report Series 10, Fisheries Victoria, Queenscliff.

McGarvey, R., Feenstra, J. (2004). Stock assessment models with graphical user interfaces for key South Australian marine finfish stocks. Final Report to FRDC (Project No. 1999/145). South Australian Research and Development Institute (Aquatic Sciences), Adelaide. 176 pp.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2012). Interannual variation in larval survival of snapper (*Chrysophrys auratus*, Sparidae) is linked to diet breadth and prey availability. Canadian Journal of Fisheries and Aquatic Sciences 69: 1340-1351.

Murphy, H.M., Jenkins, G.P., Hamer, P.A., Swearer, S.E. (2013). Interannual variation in larval abundance and growth in snapper, *Chrysophrys auratus* Sparidae, is related to prey availability and temperature. linked to diet breadth and prey availability. Marine Ecology Progress Series 487: 151-162.

Smart, J., Steer, M.A., Bailleul, F., Hall, D., Knuckey, I., Magnusson, A., Morison, J., Presser, J., Schirmer, J. (2022). Informing structural reform of South Australia's Marine Scalefish Fishery. Final Report to FRDC (Project No. 2017-014). 319 pp.