The influence of fish movement on regional fishery production and stock structure for South Australia's snapper (*Chrysophrys auratus*) fishery

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Abbreviations

ANOVA	analysis of variance
CFL	caudal fork length
GAB	Great Australian Bight
GSV	Gulf St. Vincent
IS	Investigator Straight
INC	increment number
KI	Kangaroo Island
LA-ICP-MS	laser ablation – inductively couple plasma mass spectrometry
MANOVA	multivariate analysis of variance
NGSV	Northern Gulf St. Vincent
NSG	Northern Spencer Gulf
NSW	New South Wales
PIRSA	Primary Industries and Regions SA
PPB	Port Phillip Bay
QDFA	quadratic discriminant function analysis
RI	residence index
SA	South Australia
SARDI	South Australian Research and Development Institute
SDF	standardised detection frequency
SE	south east region of South Australia
SG	Spencer Gulf
SGSV	Southern Gulf St. Vincent
SSG	Southern Spencer Gulf
SWG	Snapper Working Group
TS	transverse section
WA	Western Australia

Executive Summary

Overview

From 2007 onwards, South Australia's snapper (*Chrysophrys auratus*) fishery underwent significant and unprecedented changes that impacted on the management of the fishery. This ultimately reflected our poor understanding of the movement behaviour of snapper and its consequences for stock structure. This collaborative project that ran from 2012 to 2014 and involved SARDI and Fisheries Victoria was aimed at redressing our poor understanding of snapper movement and stock structure throughout south eastern Australia.

The study included the largest and most comprehensive application of an otolith chemistry study for snapper, as well as the first completed acoustic telemetry study on snapper in Australia. From the various findings, hypotheses were developed to account for the recent regional trends in population dynamics. Fundamentally, these relate to inter-annual variation in recruitment to the three primary nursery areas of south eastern Australia, i.e. Northern Spencer Gulf (NSG), Southern Spencer Gulf (SSG), and Port Phillip Bay, Victoria (PPB). The other regional populations of South Australia depend on supplementation through emigration from these source populations. The latter regions included: the South East (SE) which depends on recruitment into and emigration from PPB; Southern Spencer Gulf (SSG) and probably also the west coast of Eyre Peninsula (WC) that depend on emigration from Northern Spencer Gulf (NSG); and Southern Gulf St. Vincent (SGSV) that depends on movement from Northern Gulf St. Vincent. The relationship between the three nursery areas and the regions to which fish emigrate determines the stock structure. As such, the three stocks that influence fishery catches in South Australia are the SG/WC Stock, GSV Stock and Western Victorian Stocks.

Background

Snapper is a significant fishery resource of South Australia, and one of the most valuable and productive species taken in the multi-species Marine Scalefish Fishery. From 2007, there were significant changes in this fishery that caused concerns for managing the fishery. In the commercial sector there was a dramatic switch from a handline to a longline fishery that reflected the adoption of new efficient longline fishing technology. This resulted in higher catches, effort and catch rates. Simultaneously, there were significant changes in the spatial structure of the fishery. The catches and catch rates in Spencer Gulf, which had previously been the mainstay of the State's fishery, declined significantly, whilst they increased considerably in NGSV and the SE. These changes, which reflected a significant redistribution of the biomass of snapper at the regional scale, were remarkable and unprecedented.

The downturn in the fishery in SG raised considerable concern about the long-term sustainability of the recently-improved fisheries in NGSV and the SE, particularly given the high efficiency, catch rates and effort in the longline sector. Nevertheless, addressing such concerns with an appropriate management strategy was limited by our poor understanding of the demographic processes that had led to the changes and extent to which the processes in the different regions were inter-related. This primarily reflected our poor understanding of the movement behaviour of snapper and extent to which inter-regional movement could influence population dynamics. As such, there was a need to account for the recent changes in the fishery that focussed on the movement behaviour of snapper, from which inferences could be drawn about stock structure. This would point to the appropriate scale of fishery management.

Objectives

The specific objectives addressed in the study were:

1. to determine the spatial origins of snapper that occupy the different regions of South Australian waters, and determine if and when during their life histories that any large-scale movement took place to account for current patterns of dispersion. This was primarily based on a suite of otolith-based techniques;

2. to develop a better understanding of the movement behaviour of snapper at several spatial and temporal scales throughout Gulf St. Vincent using acoustic telemetry techniques;

3. to develop a better spatial management strategy for the snapper fisheries of south eastern Australia based on our enhanced understanding of inter-regional and cross-jurisdictional fish movement.

Methods

The objectives with respect to large-scale fish movement and stock structure were addressed using a ‘multiple-technique’ approach, which involved regional comparisons of numerous physical characteristics of the fish. Differences in such physical characteristics amongst populations would indicate the lack of mixing of fish between regions, consistent with separation into different stocks. These included demographic characteristics associated with populations including: size and age structures; growth functions; and inter-annual recruitment histories. Furthermore, numerous characteristics from the transverse sections of otoliths were compared amongst regions that included otolith size and clarity of the annual incremental structure. Data were also recorded from the chronological structure of the transverse sections providing age-related data that included: increment widths; optical density; and otolith chemistry. The optical characteristics of otoliths were recorded using image analysis whilst the elemental concentrations were recorded using inductively coupled plasma mass spectrometry. Otoliths from four year classes, i.e. 1991, 1997, 2001 and 2004, were considered. For each year class, similar-aged fish were considered so as to minimise the influence of inter-annual variability on otolith characteristics that were compared amongst fish from the five South Australian regions and PPB.

Fish movement at the small scale of metres to 10s of km was considered in an acoustic telemetry study in a study area of approximately 160 km^2 in NGSV. Throughout this three-year project, a total of 54 snapper were tagged with acoustic tags for which positional data were recorded using an array of up to 41 *in situ* acoustic listening stations. The positional data were interpreted in terms of seasonal patterns in fish movement and habitat use.

Results

Comparison of population-based demographic characteristics and physical and chemical characteristics of otoliths demonstrated consistent regional differences. Such results indicated that throughout south eastern Australia, snapper do not constitute a single, large, inter-mixed stock but that there is significant spatial structure to the population. Age-related data from increment width analyses and elemental concentrations provided significant insight into the regional demographic processes responsible for this structure. Regional population dynamics were primarily driven by inter-annual variation in recruitment to the three primary nursery areas of NSG, NGSV and PPB. Each of these populations is self-sustaining but is also the source of fish that subsequently emigrate to and replenish other regional populations. The numbers available for emigration vary from year-to-year, reflecting environmentally-driven, inter-annual variation, whilst the extent of movement influences stock structure.

The SE population was found to depend on emigration of snapper from PPB over a distance of approximately 600 km. The large biomass and fishery catches from this region during the period from 2008 to 2012 related to strong year classes of 2001 and 2004 in PPB, followed by emigration of thousands of fish to the SE. Through a similar process, NSG is the likely source population for SSG, as well as for the WC and Investigator Strait. The decline in biomass in NSG and SSG appears to reflect persistent high levels of exploitation in both regions, as well as poor recruitment though the 2000s. NGSV appears to support a self-sustaining population whose recent significant biomass from 2008 onwards built up through local reproduction and recruitment.

The stock structure for snapper in south eastern Australia is built around the three primary nursery areas and subsequent emigration of juvenile/adult fish. PPB is the primary source of recruitment for the Western Victorian Stock that extends westward to as far as the Fleurieu Peninsula, although the western boundary varies with year class strength. The populations of NSG and SSG constitute a single stock that also historically extended to the Eyre Peninsula and Investigator Strait. The lack of emigration from SG and PPB into GSV suggests that the latter represents a separate stock from which there is likely to be some overflow into Investigator Strait.

Implications

The SE population is part of the Western Victorian Stock, i.e. a cross-jurisdictional stock that depends on variable recruitment into PPB which drives the episodic, regional abundance, biomass and fishery productivity. As such, this regional fishery depends on the stock status in PPB, which is managed by Fisheries Victoria. The fishing industry needs to consider the most economic and efficient way of exploiting this transient resource. An indication of future catches is available from the annual recruitment surveys that are done in PPB by Fisheries Victoria.

The two stocks of SG/WC and GSV are likely to currently be classified, based on the recent stock assessment, as ‘transitional depleting’ and ‘sustainable’, respectively. As such, these two stocks could be managed in different ways pursuing different objectives, i.e. a strategy for conserving adult biomass could be applied in GSV, whilst one for rebuilding biomass could be applied for the SG/WC Stock.

The harvest strategy for SA’s snapper fishery will be formally reviewed in 2018 and will reconsider the management and/or monitoring boundaries based on the findings of this research project.

Key words

Snapper, *Chrysophrys auratus*, movement, stock structure, regional population, phenotypic characteristics, otolith, acoustic telemetry, south eastern Australia, Spencer Gulf, Gulf St. Vincent, Port Phillip Bay.

1. General Introduction

Anthony Fowler

1.1 Background

Importance of understanding stock structure

Across the range of a fish species its individuals are usually divided into a number of local populations, the ensemble of which constitutes a metapopulation (Bailey 1997). The spatial distribution of such local populations and the extent of movement of individuals between them, are determined by a range of environmental influences (Bailey 1997). In fishery science and management, it is fundamental to understand these relationships as they determine the 'stocks' and 'stock structure' that represent the base population units into which the fishery is divided. Fish stocks are defined as groups of individuals of a fish species that are essentially self-sustaining and have similar life history characteristics (Hilborn and Walters 1992, Begg and Waldman 1999). As such, stocks represent the most fundamental scale at which fishery assessment and management should be directed. Failure to recognise the appropriate stock structure has contributed to notable failures in fishery management (Stephenson 1999, Hutchinson 2008).

The stock structure for a fishery species relates to the spatial scale over which the demographic processes operate that drive the population dynamics of the individual stocks. This spatial scale is determined by a range of environmental influences that include distance, habitat patchiness and physical barriers (Bailey 1997). Whilst such biological and physical interactions determine the appropriate spatial scale at which a fishery should be managed, management is often directed at spatial scales that are convenient for political or administrative reasons (Stephenson 1999). Furthermore, it has been suggested that the failure to recognise the complex sub-structuring of fish populations has led to the repeated failure of the single species approach to fishery management and the poor status of many of the world's fisheries. This is because applying fishery management at the wrong spatial scale can lead to local populations being fished at levels that they demographically cannot sustain, ultimately leading to localised depletion of the fishery resource (Bailey 1997, Hutchinson 2008).

Determining the stock structure for a fish species is extremely challenging as it depends on understanding the spatial scales of movement of individuals during the different life history stages. This can be further complicated by the complex demographics of marine fishes, driven by spatial and temporal variability in recruitment patterns, as well as the fact that environments of marine ecosystems around the world are changing (Hutchinson 2008). The process of determining stock structure involves drawing inferences about the level of interaction amongst regional populations based on comparisons of their genotypes and/or phenotypic characteristics (Begg et al. 1999, Begg and Waldman 1999). Genotypic and phenotypic differences amongst populations relate to separation over different time scales (Pawson and Jennings 1996). The former indicate the consequence of natural selection over evolutionary time scales, whilst the latter indicate the lack of movement between local populations at ecological time scales. Phenotypic differences do not necessarily imply genetic differences since the movement of a few individuals per generation between local populations can sustain genetic homogeneity, even though they are essentially ecologically separated (Bailey 1997). Also, population structure may change over time, depending on fluctuations in population abundance and recovery from over-exploitation (Baldwin et al. 2012). Given such complexities, it has been recommended that to confidently determine the stock structure for a fish species, a holistic or 'multiple-technique' approach should be used (Begg et al. 1999, Begg and Waldman 1999, Abaunza et al. 2008, Baldwin et al. 2012).

Snapper in south eastern Australia

Taxonomy, distribution and stock structure

Snapper (*Chrysophrys auratus*) is a large, long-lived, demersal finfish species that is a member of the family Sparidae (Percirforms: Percoidei). The species is broadly distributed throughout the Indo-Pacific region including Japan, the Philippines, India, Indonesia, New Zealand and Australia (Kailola et al. 1993). It has a broad Australian distribution that includes the coastal waters of the southern two thirds of the continent, including southwards from the mid-coast of Western Australia, southern continental coastline, and east coast as far as north Queensland (Kailola et al. 1993, Jackson et al. 2012). Also, for a long time, snapper have been found along the north coast of Tasmania and in recent years have extended their range to southern Tasmania (Last et al. 2011). Snapper occupy a diversity of habitats from shallow, demersal areas to the edge of the continental shelf across a depth range of 1 – 200 m. Each of the Australian mainland states supports important fisheries for this species (Anon 2012, 2013, Fowler et al. 2014). It is unusual for an Australian marine fish species to have such a broad geographic distribution and economic significance. Furthermore, snapper is a prime target species of the recreational and charter boat sectors of each state. These characteristics make snapper one of Australia's most significant fishery resources.

A number of studies have indicated that across its Australian range, snapper is divided into several separate stocks. One division occurs at Wilson's Promontory in Victoria from where the East Coast Stock extends 2000 km up the coast of New South Wales to north Queensland (Sanders 1974). Then, the Western Victorian Stock is thought to extend westwards from Wilson's Promontory into the waters of south eastern South Australia (SA), and to include the important fishery and nursery area of Port Phillip Bay (Donnellan and McGlennon 1996). This finding is based on the analysis of allozymes, mitochondrial DNA and tagging data which indicate a broad stock division between the Western Victorian and the South Australian Stocks in the vicinity of the mouth of the Murray River. For the South Australian Stock that is distributed across >2000 km of heterogeneous coastline and a diversity of habitats throughout the waters of Gulf St. Vincent

(GSV), Investigator Strait (IS), Spencer Gulf (SG), and the Great Australian Bight (GAB), there is no evidence for any finer-scale genetic differentiation (Donnellan and McGlennon 1996).

The extensive geographic ranges of the three stocks throughout eastern, south eastern and southern Australia contrast with the complex, fine-scale stock structure of Shark Bay in Western Australia, for which there is evidence of minimal exchange of fish amongst populations over relatively short distances of 10s of km both within and outside the bay (Edmonds et al. 1999, Bastow et al. 2002). This unusual situation may relate to the particularly strong salinity gradients in Shark Bay (Bastow et al. 2002). Nevertheless, it warns that fine-scale stock structure for snapper may also be a feature in the gulfs of SA.

South Australia's snapper fishery

Snapper support important commercial and recreational regional fisheries across most of SA's inshore waters (Fowler et al. 2013). Historically, the State-wide commercial catch has varied cyclically with the cycles encompassing a number of years, i.e. increasing for several years and then decreasing again (Fig. 1.1). Since 1984, there have been three such cycles, with the most recent minimum annual catch taken in 2003. From 2004, the State-wide catch increased annually to the extent that from 2007 to 2011 the highest ever annual commercial catches were recorded. Through this period, SA became the dominant State-based contributor to the national commercial catch (Fig. 1.2). SA's contribution was at its highest in 2010/11, when the commercial catch approached 1,000 t, worth in excess of $6.5 million (Knight and Tsolos 2012, Fowler et al. 2013). On the basis of these recent high annual catches, snapper became the most valuable and productive species by weight for SA's Marine Scalefish Fishery (Fowler et al. 2013). However, some concerns for managing SA's snapper fishery emerged through this period (Fowler et al. 2010). First, there was a dramatic switch from commercial handline to new longline fishing technologies, which increased the effectiveness of the fishers and resulted in higher catch rates. This attracted more fishers to target snapper which resulted in an increase in targeted fishing effort. Concomitant with these gear changes there was a dramatic change in the spatial structure of the fishery. Prior to 2003, the relatively small region of Northern Spencer Gulf (NSG) had generally contributed >50% of the State's catch (Fig. 1.1). For a few years during the mid- 2000s, Southern Spencer Gulf (SSG) dominated the catches, but from then on, the combined annual catch of NSG and SSG declined annually dropping to its lowest levels in 2012 and 2013 (Fowler et al. 2013, Fowler and McGarvey 2014). Concomitantly, there were exponential increases in catches and catch rates in several other regions, notably Northern Gulf St. Vincent (NGSV) and the South East (SE). These regions largely accounted for the record State-wide catches from 2009 to 2012. Subsequently, NGSV has maintained its record catches whilst those from the SE declined in 2012 and 2013. The declines in catches from NSG and SSG from 2007 to the low levels in 2013 raised concern about the long-term sustainability of the snapper fishery in NGSV, particularly given the recent record levels of longline fishing catch, effort and CPUE in this region (Fowler et al. 2013, Fowler and McGarvey 2014).

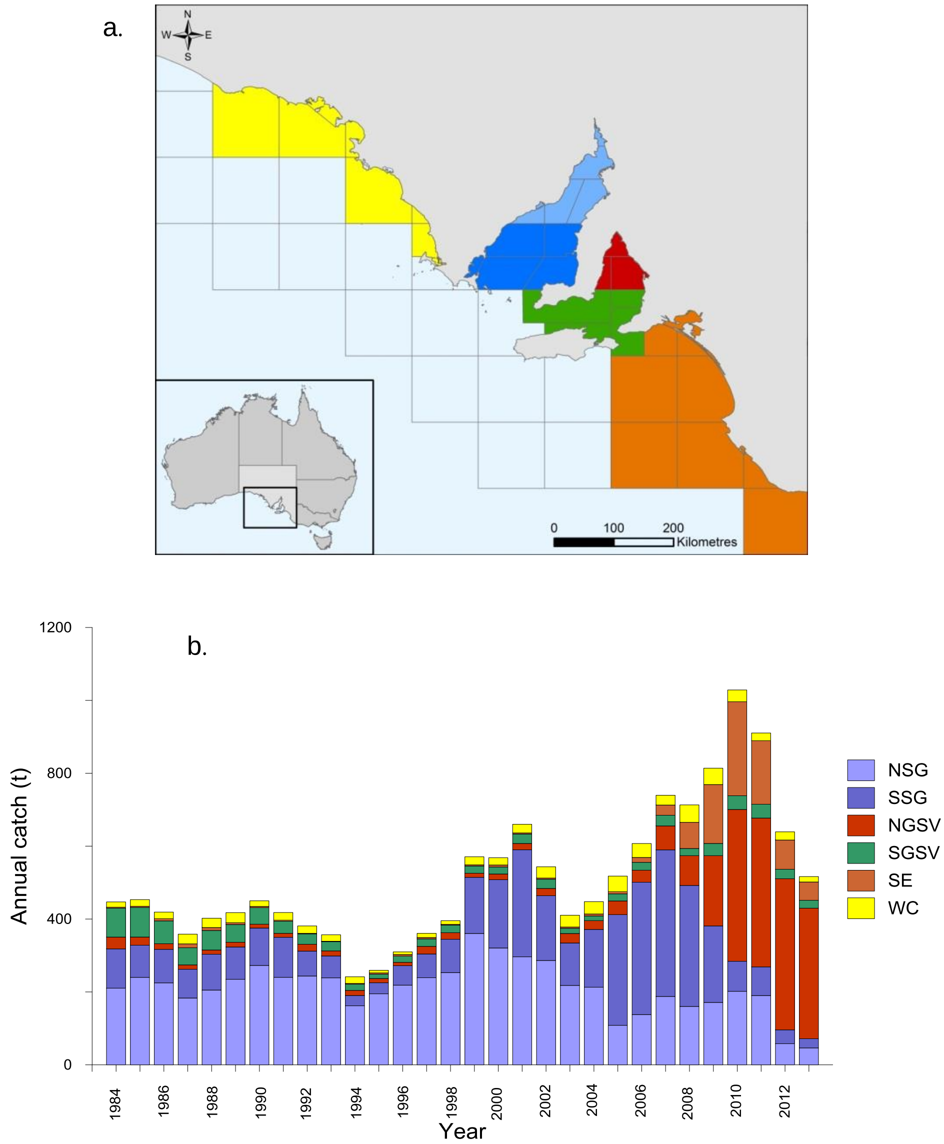

Fig. 1.1 Spatial information for South Australia's snapper fishery. a. Map of South Australia showing six coastal regions. b. Figure showing the annual commercial catches taken in the six regions since 1984. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, WC – West Coast.

In 2011, PIRSA Fisheries and Aquaculture responded to concerns about sustainability of the regional snapper fisheries in SA by establishing the Snapper Working Group (SWG) to review the fishery and its management strategy. The SWG involved representatives from the commercial and recreational fishing sectors, industry representatives, as well as fishery managers and scientists. Its discussions highlighted that our poor understanding of some aspects of the population biology of snapper limited our ability to account for the recent dramatic changes in the spatial structure of the fishery. If fish movement was involved in the regional changes in fishery productivity it would have involved many thousands of fish moving over distances of 100s of km. It was unknown whether such a phenomenon that had the potential to influence regional fishery production was possible. As such, the demographic processes that drove the dramatic regional changes in fishery productivity were not understood. Until this could be resolved, understanding the life history, stock structure, population dynamics, demography and appropriate approach to fishery management for snapper in SA would remain uncertain. For the individual regions, there were alternative hypotheses to account for the recent trends. For NGSV, the recent record level of fishable biomass may have eventuated from fish immigrating from elsewhere, possibly SG, or the biomass may have built up over several years based on local reproduction and recruitment. The concomitant decline in biomass in SG from 2008 onwards may have reflected either the failure of recruitment over numerous years or emigration from this gulf. For the SE region, large numbers of fish may have moved into this region from one of the major nursery areas that are located 100s of km to either the west or east.

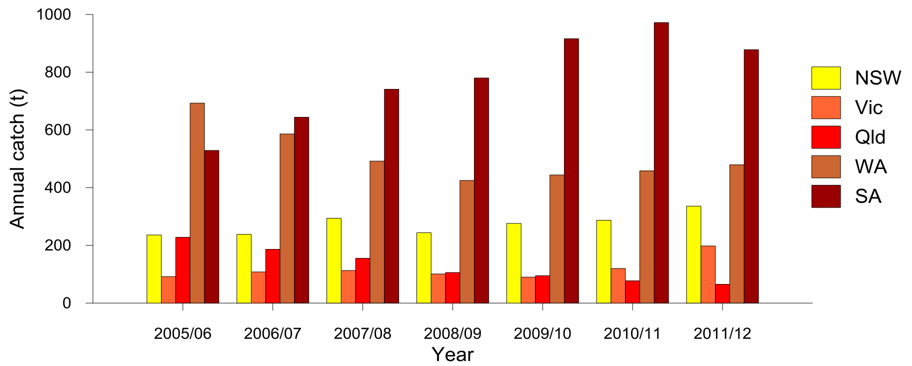

Fig. 1.2 Annual commercial catches of snapper for seven financial years from each of the five mainland states of Australia (Anon 2012, 2013). NSW – New South Wales, Vic – Victoria, Qld – Queensland, WA – Western Australia, SA – South Australia.

Determining the demographic processes that have driven the recent spatial dynamics in fishery productivity depends on elucidating the regions of origin and subsequent movement patterns of the fish. These issues around the spatial scale over which demographic processes have operated relate to the stock structure of snapper throughout south eastern Australia. As such, addressing the questions presented above about regional demographic processes to account for the dynamics in fishery productivity should enhance our understanding of the demographic processes that contribute to regional population dynamics and point to whether our current understanding of stock structure is supported in the face of the changes in the fishery. This will point to whether the spatial scales at which management is directed in the South Australian and Victorian fisheries should be reconsidered.

1.2 Need

Developing a comprehensive understanding of the movement patterns and stock structure of a fish species is crucial for identifying the appropriate scale and strategy for management.

In south eastern Australia, there are several adjacent snapper fisheries operating in SA, Victorian and Commonwealth waters that are managed using different strategies. The SA fishery, currently Australia's largest commercial snapper fishery, is divided into contiguous regions whose relative contributions to total catch have changed in recent years. The extent to which the different regional and jurisdictional populations represent a single or multiple stocks is poorly understood, because of our limited understanding of the patterns of snapper movement. For example, recent high catches of snapper from NGSV and SE may have resulted from high levels of biomass built up through local demographic processes. Alternatively, fish may have moved in from adjacent regions or possibly even from Victorian or Commonwealth waters. If large-scale movement is involved, it must be temporally complex as it appears to not conform to a regular, annual pattern. The need here is to elucidate the regions of origin and movement patterns of fish that currently contribute to high regional catches in SA to inform about the demographic processes that drive the spatial and temporal variation in fishery productivity. This will point to the appropriate spatial scale for management and provide insight for resource allocation amongst the different fisheries, which is currently being considered by the Australian Fisheries Management Forum to improve resource sharing arrangements for snapper.

1.3 Objectives

The specific objectives addressed in this study were:

1. to determine the spatial origins of snapper that occupy the different regions of South Australian waters, and determine if and when during their life histories that any large-scale movement took place to account for current patterns of dispersion. This was primarily based on a suite of otolith-based techniques;

2. to develop a better understanding of the movement behaviour of snapper at several spatial and temporal scales throughout Gulf St. Vincent, using acoustic telemetry techniques;

3. to develop a better spatial management strategy for the snapper fisheries of south eastern Australia based on our enhanced understanding of inter-regional and cross-jurisdictional fish movement.

The proposed objectives were considered using several different technological approaches for addressing questions about fish movement and stock structure at different spatial and temporal scales. First, in Chapter 2, demographic characteristics of different regional populations in South

Australia were compared. Differences in such phenotypic characteristics amongst populations would indicate the lack of mixing of fish between regions and would be consistent with separation into different stocks. Then, in Chapters 3 and 4, otolith-based techniques were used to address questions about the spatial origins of fish and possible inter-regional movement through their lives. The conceptual basis of this approach is that the otoliths from conspecific fish that have lived in different environments can manifest differences in chemistry, shape, microstructure and optical characteristics (Panfili et al. 2002), which can be used to assess whether fish have occupied different environments (Campana 1999). The final empirical approach was acoustic telemetry (Chapter 5), where internal acoustic tags and remote *in situ* listening stations were used to record positional data of tagged fish that were subsequently interpreted in terms of movement behaviour (Heupel et al. 2006). This methodology helped develop some understanding of movement behaviour at relatively small spatial and temporal scales, i.e. up to 10s of km over months to several years. This acoustic telemetry work was done in NGSV, where the biomass and fishery catches were relatively high throughout the data collection period.

2. Demographic characteristics

Anthony Fowler, Matthew Lloyd, Bruce Jackson

2.1 Introduction

South Australia's (SA) snapper fishery has undergone considerable change over the past decade. Significant variation was evident in fishery production with record catches taken in several years between 2007 and 2012 (Fowler et al. 2013) (Fig. 2.1). This temporal variation was associated with a significant change to the spatial structure of the fishery. From 2007, the catches from the traditional snapper fishery regions of Northern Spencer Gulf (NSG) and Southern Spencer Gulf (SSG) declined annually to their lowest recorded levels in 2012 and 2013 (Fig. 2.1). However, concomitant increases in catches from Northern Gulf St. Vincent (NGSV) and the South East (SE) produced record catches and largely accounted for the record State-wide catches.

The spatial and temporal changes in the snapper fishery caused significant management concerns. These concerns were ultimately based on our poor understanding of the demographic processes responsible for the changes, particularly with respect to the movement behaviour of snapper, and its influence on regional fishery production and stock structure. The underlying issue was whether the regional spatial dynamics were driven by inter-regional movement of large numbers of fish or whether different demographic processes occurred independently and contemporaneously in the different regions.

The dilemma about the causes of the recent spatial dynamics for snapper in SA is based around whether or not fish partake in large-scale, inter-regional movement. As such, this is a stock structure issue. The accurate determination of stock structure for any fishery species is a fundamental part of its assessment and management. To achieve this, a 'multiple-technique' approach has been recommended (Begg and Waldman 1999). One such approach is the comparison of demographic characteristics amongst populations. If adjacent local populations have similar characteristics in terms of size and age structures, growth characteristics and recruitment patterns, then there may be sufficient inter-population movement of individuals for them to constitute a single stock. Alternatively, if there are significant differences in at least some demographic characteristics, then the populations may be sufficiently isolated to constitute separate stocks.

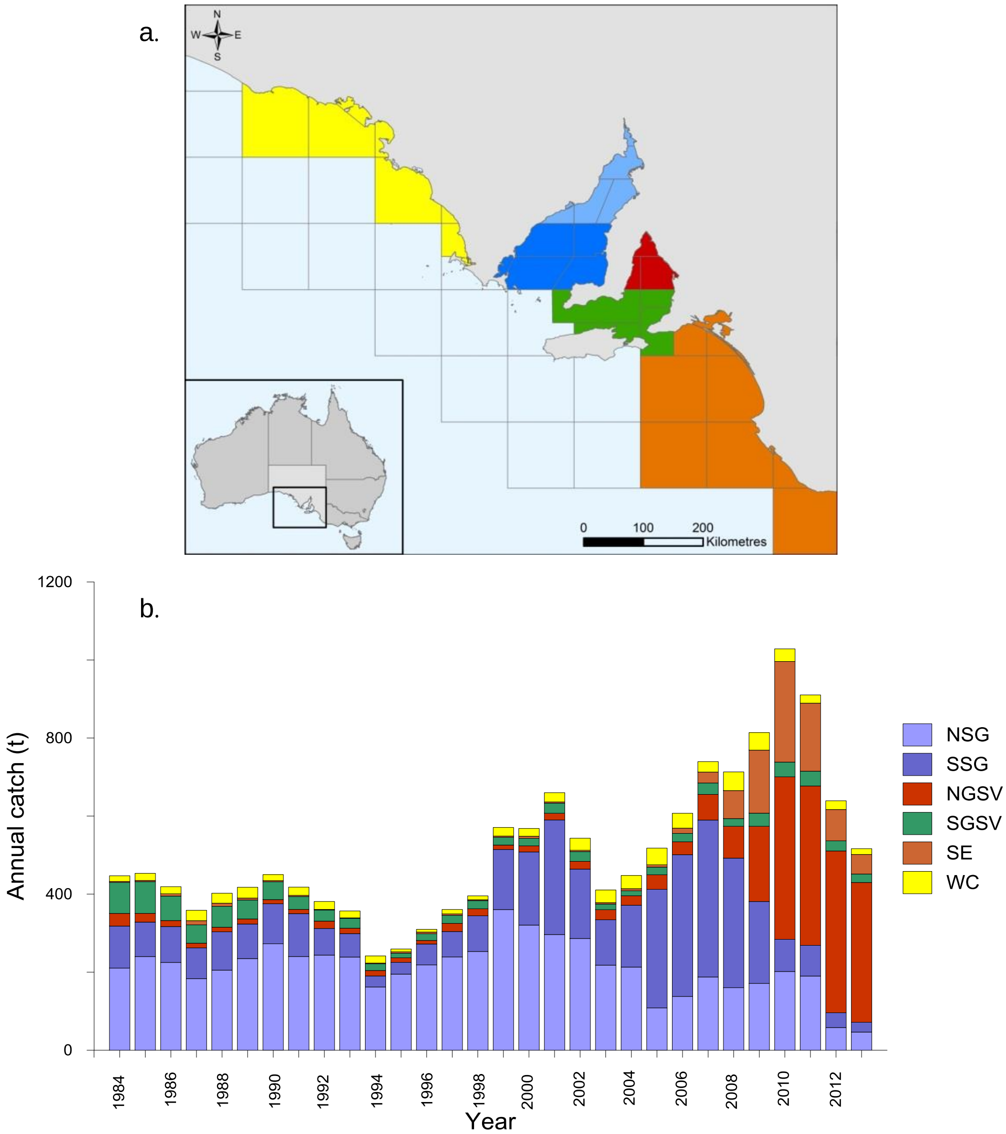

Fig. 2.1 Spatial information for South Australia's snapper fishery. a. Map of South Australia showing the six coastal regions. b. Figure showing the annual commercial catches taken in the six regions since 1984. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, WC – West Coast.

The aim of this chapter was to compare the demographic characteristics amongst a number of regional populations of snapper in South Australia, and interpret the results in terms of likely separation between them. The regional populations considered were; NSG, SSG, NGSV, Southern Gulf St. Vincent (SGSV) and the SE. This analysis was based on the results from SARDI's market sampling program that has operated since 2000. The comparison of population characteristics was largely done between two three-year periods that represent different stages in the recent history of SA's snapper fishery. The first period is 2001 to 2003, when record catches were taken from NSG and SSG, but small or incidental annual catches were recorded from NGSV and the SE, respectively (Fig. 2.1). The second period is from 2009 to 2011, when catches in each of NSG and SSG had declined considerably and record catches were taken from NGSV and the SE that sustained the annual State-wide catch at a record level. The parameters that were compared amongst regions and between time periods in this study were: population size and age structures; growth curve parameters; and recruitment histories.

2.2 Methods

2.2.1 Market sampling

For the calendar years of 2000 to 2003 and 2007 to 2012, as well as the financial year of 2005/06, market sampling was undertaken for the catches of snapper taken by the commercial sector of SA's Marine Scalefish Fishery. Market sampling was concentrated at the SAFCOL wholesale fish market in Adelaide, SA. Catches of snapper landed at regional ports around SA are trucked overnight to this market, to be auctioned early the next morning. Our approach to market sampling conformed to a two-stage sampling protocol (Quinn and Deriso 1999). SARDI staff visited the fish market once per week and processed catches of snapper prior to the auction. Catches were selected for processing to ensure as broad a geographic range as possible. Fish from these catches were measured for caudal fork length (CFL) to the nearest mm, using a fish measuring board. Then, the otoliths from some fish were removed for later ageing work, with numbers approximately in proportion to their frequencies in the different size classes. The fisher and processing date for each catch were recorded so that the fishing method and Marine Fishing Area could be accessed later from the catch return once submitted by the fisher (Fowler et al. 2013).

2.2.2 Fish Ageing

A consistent fish ageing technique was used throughout the market sampling program (McGlennon et al. 2000). One sagitta from each fish was embedded in resin and a transverse section was removed using a diamond saw, and then glued to a glass microscope slide using super glue. The transverse (TS) section was examined with a low-power binocular microscope (10-20x), illuminated with transmitted light and its macrostructure, consisting of annual increments, was interpreted by counting the opaque zones. Furthermore, a qualitative estimate of the width of the marginal increment was recorded. Fish age was then estimated from; the number of opaque zones, width of the marginal increment, sample date, and a universal birth date of 1st January that approximates the middle of the spawning season (Saunders et al. 2012). The annual periodicity of increment formation in the otoliths of snapper was validated using 'otolith edge' analysis and marginal increment analysis for South Australian fish (McGlennon et al. 2000; Fowler and Schilling 2004), and from elsewhere (Ferrell et al. 1992, Francis et al. 1992). Throughout the early 2000s, quality control for the fish ageing program involved comparing fish age estimates between two experienced otolith readers (McGlennon et al. 2000). However, during the later sampling period, a single otolith reader was used, who tested his otolith interpretation against a reference collection of snapper otoliths every three months. The average percent error across these sampling occasions was 1.74% (±0.77), which is low for a species with an age structure that involves approximately 30 age classes. To date, there has been no systematic bias evident in any testing against the reference collection.

2.2.3 Data processing

Generation of size and age structures

The estimates of fish size and age from the market sampling were used to develop annual, regional size and age structures using the computational procedures developed by Davis and Walsh (1995), which have been used regularly since 1997 (McGlennon et al. 2000, Fowler and McGlennon 2011, Fowler et al. 2013). First, an annual size structure was developed for each region based on all fish measured during each year regardless of whether captured by handline or longline, but weighted according to the sizes of the catches by the two gear types. The sizes of snapper were considered in four categories, i.e. 'small' (30 – 40 cm CFL), 'medium' (40 – 60 cm CFL), 'large' (60 – 80 cm CFL), and 'very large' (>80 cm CFL).

An age/length key was generated for each region and year, based on the specific size-at-age data collected in that year. Then the age/length key was applied to the length frequency distribution to generate an annual, region-specific age structure. The regional size and age structures were compared between the two periods of 2001 to 2003 and 2009 to 2011.

Growth analysis

For each of the five regions, the size-at-age data collected from 2001 to 2003 and 2009 to 2011 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 generate estimates of L_∞, K and t_0. Then, for each period, the von Bertalanffy growth parameters were compared between regions. This was done graphically based on estimating the 95% confidence ellipses around the estimates of L_∞ and K using R and the method of Kimura (1980).

Development of recruitment histories

The numerous annual age structures developed for each region from market sampling between 2000 and 2012 were used to generate a recruitment time-series for that region. For each annual age structure, year class strength was estimated using a catch curve regression that was fitted to the natural log of the numbers of fish per age class (Maceina 1997, Staunton-Smith et al. 2004, Jenkins et al. 2010). The residuals, i.e. the deviations of the observed counts from the expected abundances determined from the regression equation were assumed to reflect the variation in year class strength, i.e. large positive and negative residuals represented strong and weak year classes, respectively. The regression analyses were restricted to the 4+ age class and older, in order to minimise any bias from the under-representation of younger age classes that had not fully recruited to the fishery. Then, for each region, an average recruitment time series was calculated from the numerous annual recruitment time series.

2.3 Results

2.3.1 Size and age structures

Northern Spencer Gulf

From 2001 to 2003, NSG produced near record catches (Fig. 2.1), which accounted for most fish that passed through the SAFCOL fish market and the strongest contribution to our market sampling. The resulting annual size distributions were based on a minimum of 4,000 fish measured per year, and each involved several different size modes (Fig. 2.2). In each year, the 'small' size class was the most numerous, whilst there were also modes of 'medium' and 'large' fish. In 2001 and 2002, the catches were dominated by the strong 1991 and 1997 year classes, whilst in 2003 the strong 1999 year class also emerged (Fig. 2.2). These three strong year classes largely accounted for the annual variation in the size structures, i.e. across the three years, the 'large' fish primarily related to the strong 1991 year class, whilst the 'small' fish were at first relatable to the 1997 and subsequently to the 1999 year class.

During 2009 to 2011, the catches from NSG had dropped considerably from the earlier record levels (Fig. 2.1), which meant that fewer fish from this region were passing through the SAFCOL market making fewer available for our market sampling (Fig. 2.2). The size distributions were variable between years, but consistently included fewer 'small' fish than in the earlier years. The dominant year classes that contributed to the age structures through this period remained the 1997 and 1999 year classes, which together accounted for most of the 'large' fish sampled through this period. The contributions of the 2004 and 2006 year classes were inconsistent between the three years. The declining biomass reflected the lack of persistence of any strong year classes subsequent to the 1999 year class.

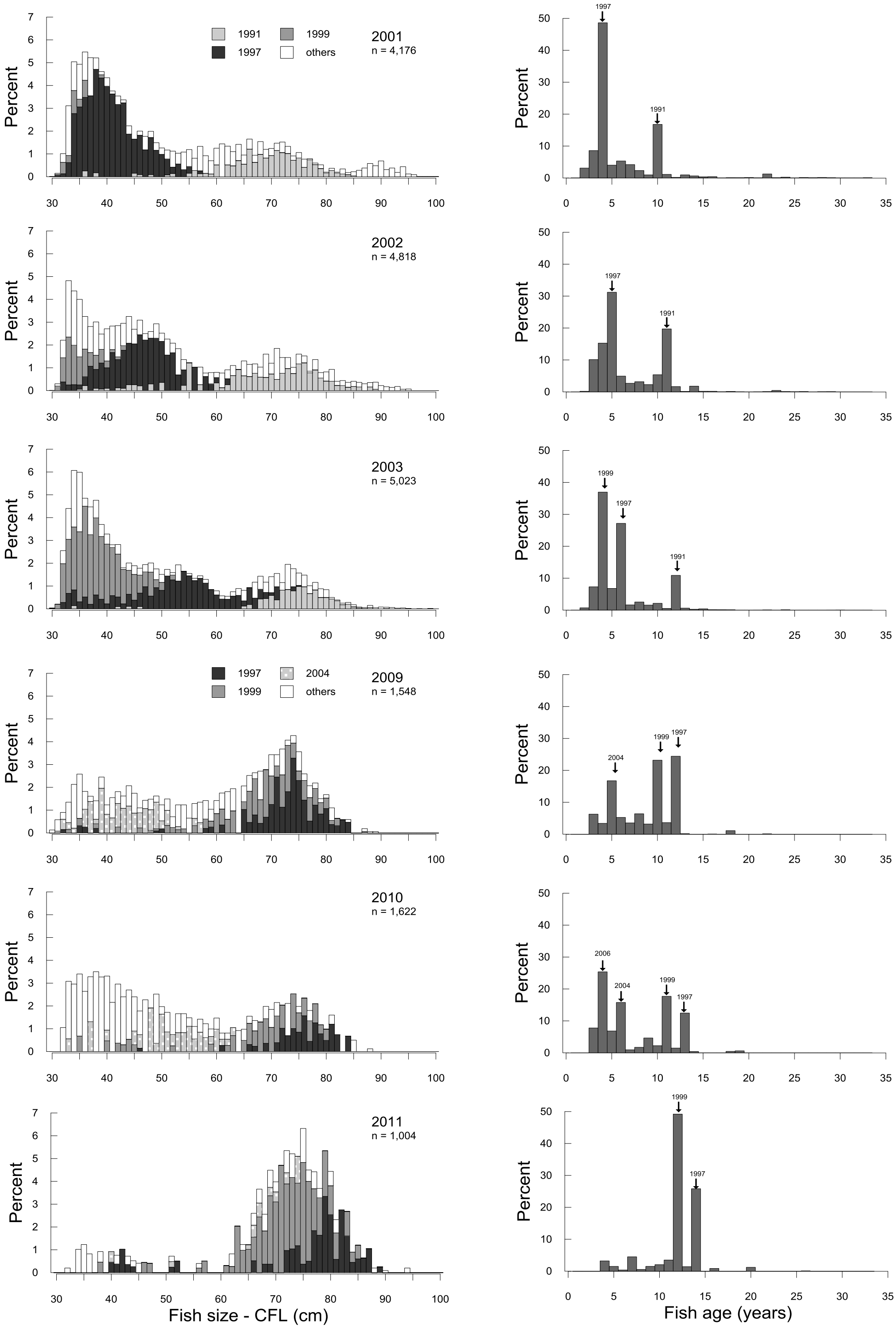

Fig. 2.2 Estimated size and age structures for snapper in Northern Spencer Gulf based on market sampling during the two periods of 2001 to 2003 and 2009 to 2011. For the size structures (left hand graphs), the contributions of particular year classes are indicated by shading. For the estimated age structures (right hand graphs), strong year classes are identified.

Southern Spencer Gulf

From 2001 to 2003, the numbers of fish measured from SSG were substantially higher than from the latter period because of the higher catches and numbers of fish that passed through the SAFCOL market. The size distributions essentially reflected modes of ‘small’ and ‘large’ fish (Fig. 2.3), and so were simpler than those from NSG. The age structures were also relatively simple, reflecting the dominance of a few year classes. In 2001 and 2002, the age structures were dominated by the 1991 year class, with emerging significance of the 1997 year class. In 2003, the 1997 year class was strongest whilst the 1999 year class was emerging. Fish from the different year classes did not form discrete size modes, as was the case with NSG. Rather, those fish from older age classes were represented by individuals across the broad size range from ‘small’ to ‘large’.

From 2009 to 2011, the numbers of fish sampled from this region were considerably fewer than during the earlier period due to the lower catches (Fig. 2.3). The size structures were represented by fish distributed across the range of ‘small’, ‘medium’ and ‘large’ categories (Fig. 2.3). The three age distributions consistently reflected the dominance of only the 1997 and 1999 year classes, with no subsequent persistent strong year class. The sizes of fish in the two strong year classes were distributed across the three size categories suggesting that the declining biomass of snapper in SSG was associated with the lack of recruitment of a strong year class subsequent to that of 1999.

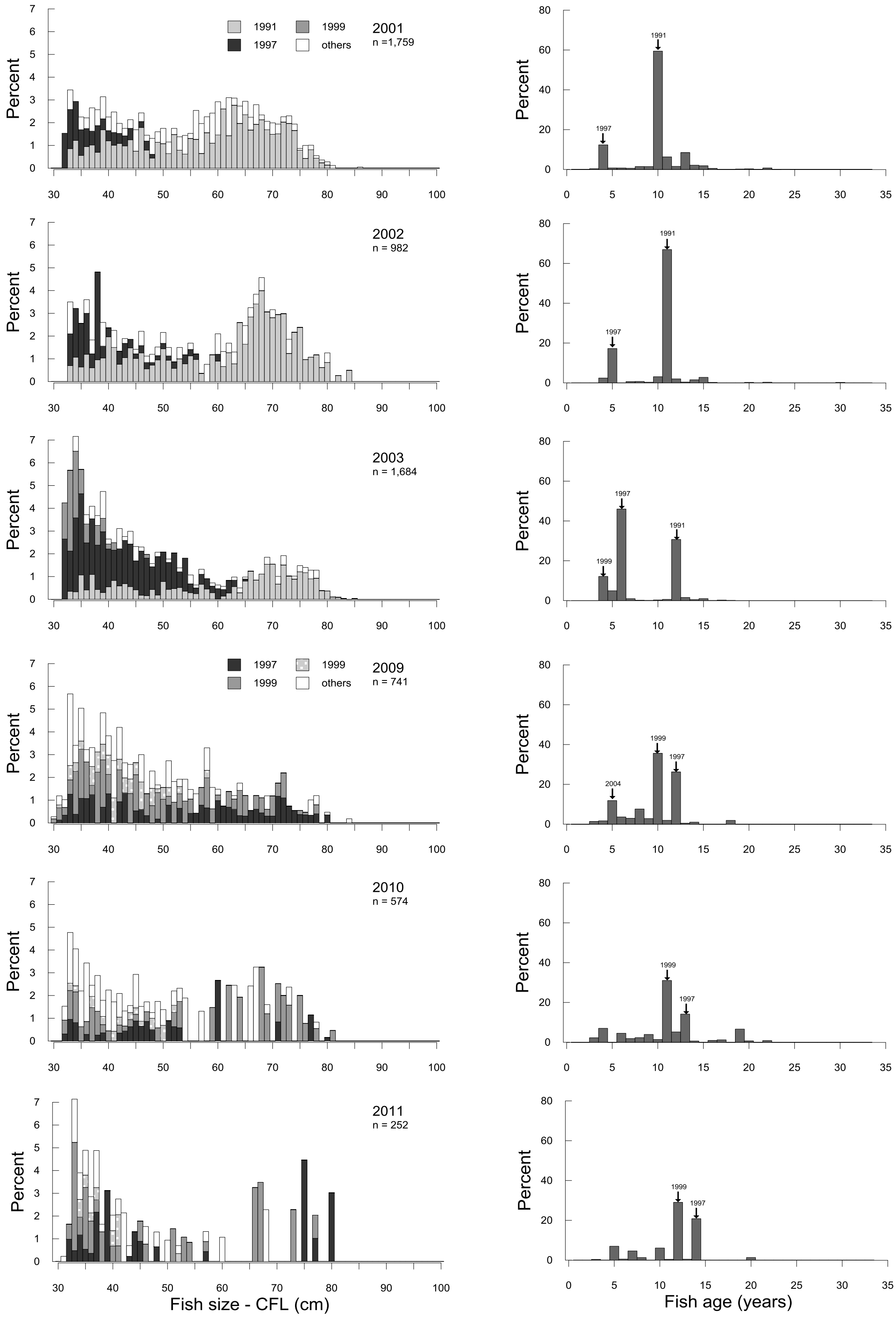

Fig. 2.3 Estimated size and age structures for snapper in Southern Spencer Gulf based on market sampling during the two periods of 2001 to 2003 and 2009 to 2011. For the size structures (left hand graphs), the contributions of particular year classes are indicated by shading. For the estimated age structures (right hand graphs), strong year classes are identified.

Northern Gulf St. Vincent

The numbers of fish from NGSV that were measured and aged from 2001 to 2003 were extremely low, i.e. <200 fish per year, reflecting the very low commercial catches through this period (Fig. 2.1). These low catches were dominated by 'large' fish predominantly from the 1991 year class (Fig. 2.4).

Between 2009 and 2011, the numbers of fish measured increased to >3,000 fish.year^{-1}. 'Large' and 'very large' fish dominated the size structures in 2009 and 2010 whilst all size classes were well represented in 2011 (Fig. 2.4). Numerous strong year classes were evident in the age structures, i.e. the 1991, 1997, 1999, 2001, 2004 and 2006 year classes. These year classes formed relatively discrete size modes, and influenced the shape of the size distributions. The high biomass of snapper through this period reflected these numerous strong year classes.

Southern Gulf St. Vincent

Commercial catches of snapper from SGSV have generally been lower than those from both NSG and SSG as well as the recent catches from NGSV. Nevertheless, they did increase marginally between the periods of 2001 - 2003 and 2009 - 2011 (Fig. 2.1). The sample sizes measured through both periods, i.e. several hundred fish per year, were relatively low (Fig. 2.5). Through the first period, the size structures were dominated by 'large' fish, primarily relating to strong representation of the 1991 year class in the annual age structures. The 'small' and 'medium' fish were largely related first to the 1997 year class, and then to 1999 year class.

From 2009 to 2011, the size structures were dramatically different to the earlier period as they were dominated by 'small' and 'medium' fish (Fig. 2.5). They reflected three strong year classes of 2001, 2004 and 2006. The former largely accounted for the 'medium' fish through this period. The lack of fish from the 1990s accounted for the few 'large' fish and absence of 'very large' fish from the region.

South East

For the SE region, annual size and age structures are only available from 2009 to 2011, due to the substantial increase in commercial catches from 2008 onwards. These size structures were dominated by 'small' and 'medium' fish, and rarely involved any fish >60 cm CFL (Fig. 2.6). The age structures were dominated only by the 2001 and 2004 year classes. The former largely accounted for the 'medium' fish, whilst the latter largely accounted for the 'small' fish. The increase in fishable biomass in this region clearly reflects the recruitment of these two strong year classes to the population.

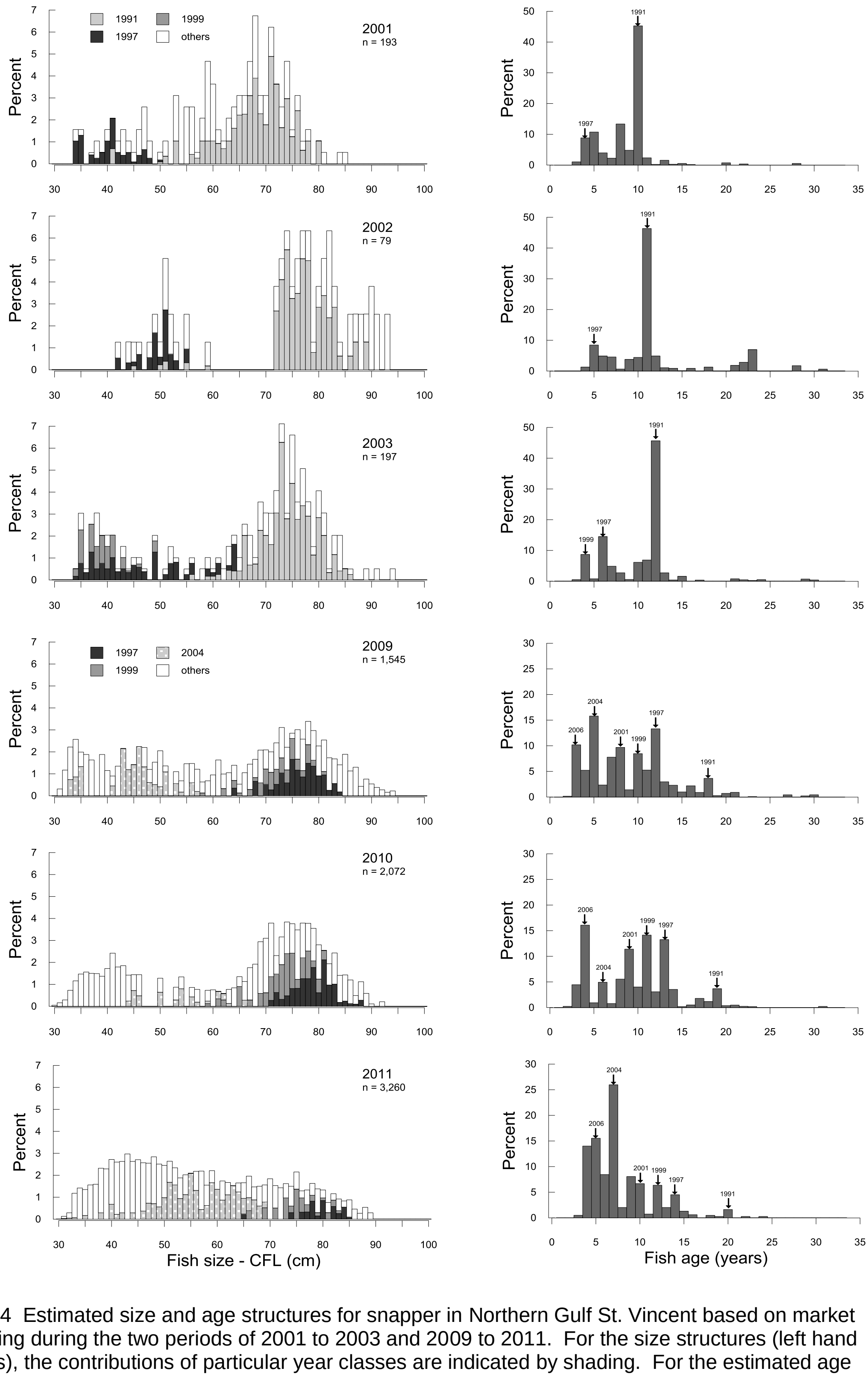

Fig. 2.4 Estimated size and age structures for snapper in Northern Gulf St. Vincent based on market sampling during the two periods of 2001 to 2003 and 2009 to 2011. For the size structures (left hand graphs), the contributions of particular year classes are indicated by shading. For the estimated age structures (right hand graphs), strong year classes are identified.

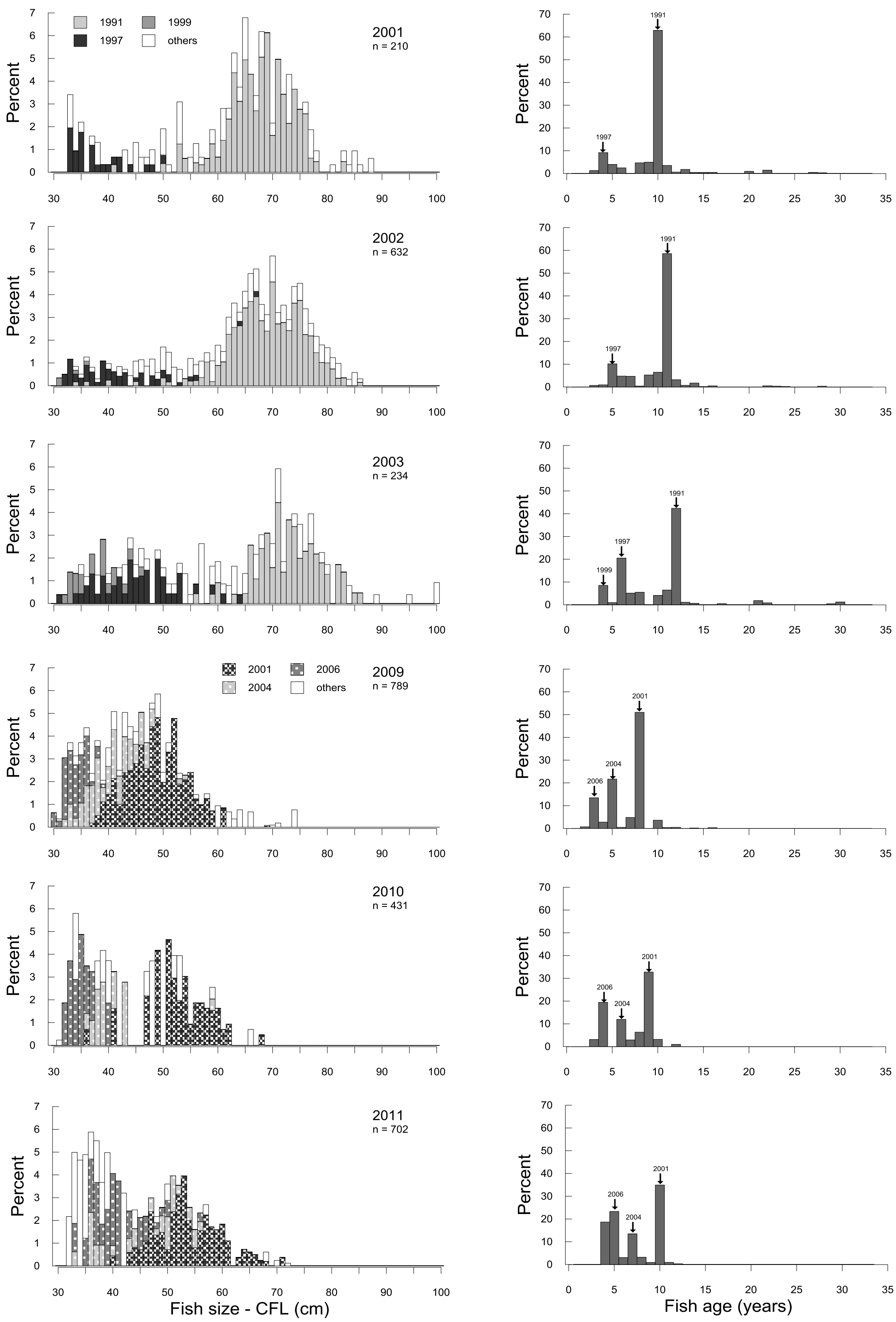

Fig. 2.5 Estimated size and age structures for snapper in Southern Gulf St. Vincent based on market sampling during the two periods of 2001 to 2003 and 2009 to 2011. For the size structures (left hand graphs), the contributions of particular year classes are indicated by shading. For the estimated age structures (right hand graphs), strong year classes are identified.

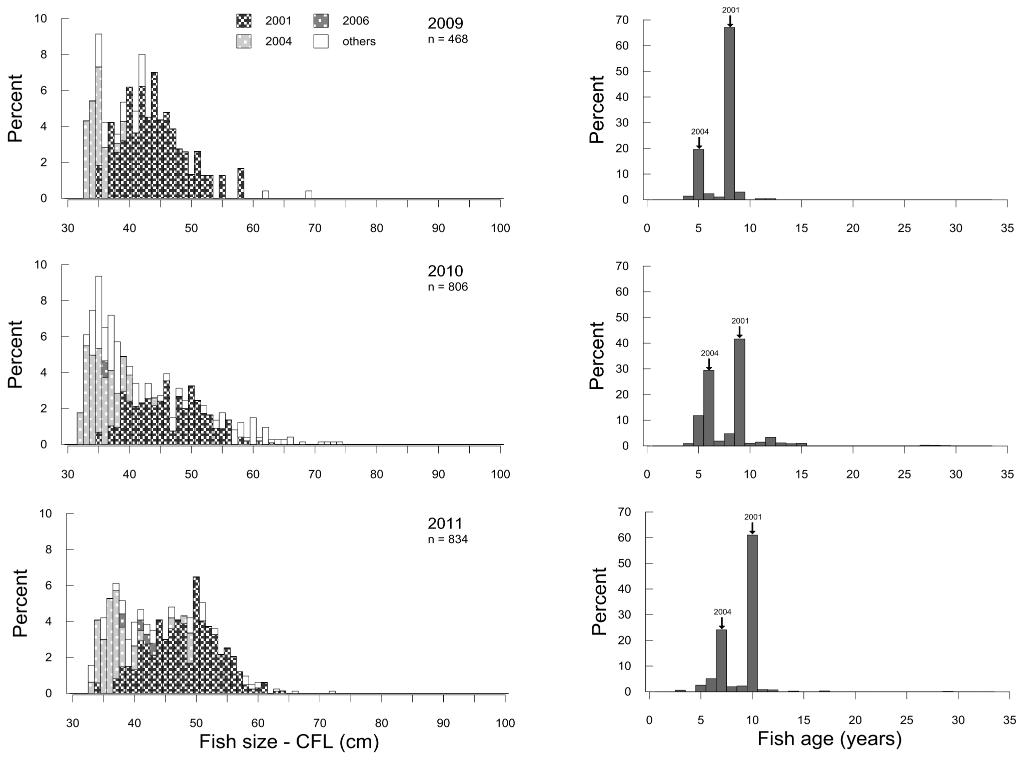

Fig. 2.6 Estimated size and age structures for snapper in South East based on market sampling from 2009 to 2011. For the size structures (left hand graphs), the contributions of particular year classes are indicated by shading. For the estimated age structures (right hand graphs), strong year classes are identified.

2.3.2 Analysis of growth

For 2001 to 2003, the estimates of size-at-age differed amongst regions (Fig. 2.7). The two northern gulfs involved more older and larger fish than did the southern regions. For SSG, relatively few fish that were >15 years of age were captured. Furthermore, for the two southern gulfs, the estimates of size-at-age were generally distributed across broader size ranges due to the presence of numerous fish that were small for their ages relative to the northern gulfs. As such, there were considerable differences in the regional estimates of growth parameters (Table 2.1). NSG, NGSV and SGSV had considerably higher estimates of L_∞ and lower values of K than SSG. There was no overlap in the 95% confidence ellipses amongst the four regions, indicating significant regional differences in growth parameters (Fig. 2.8a).

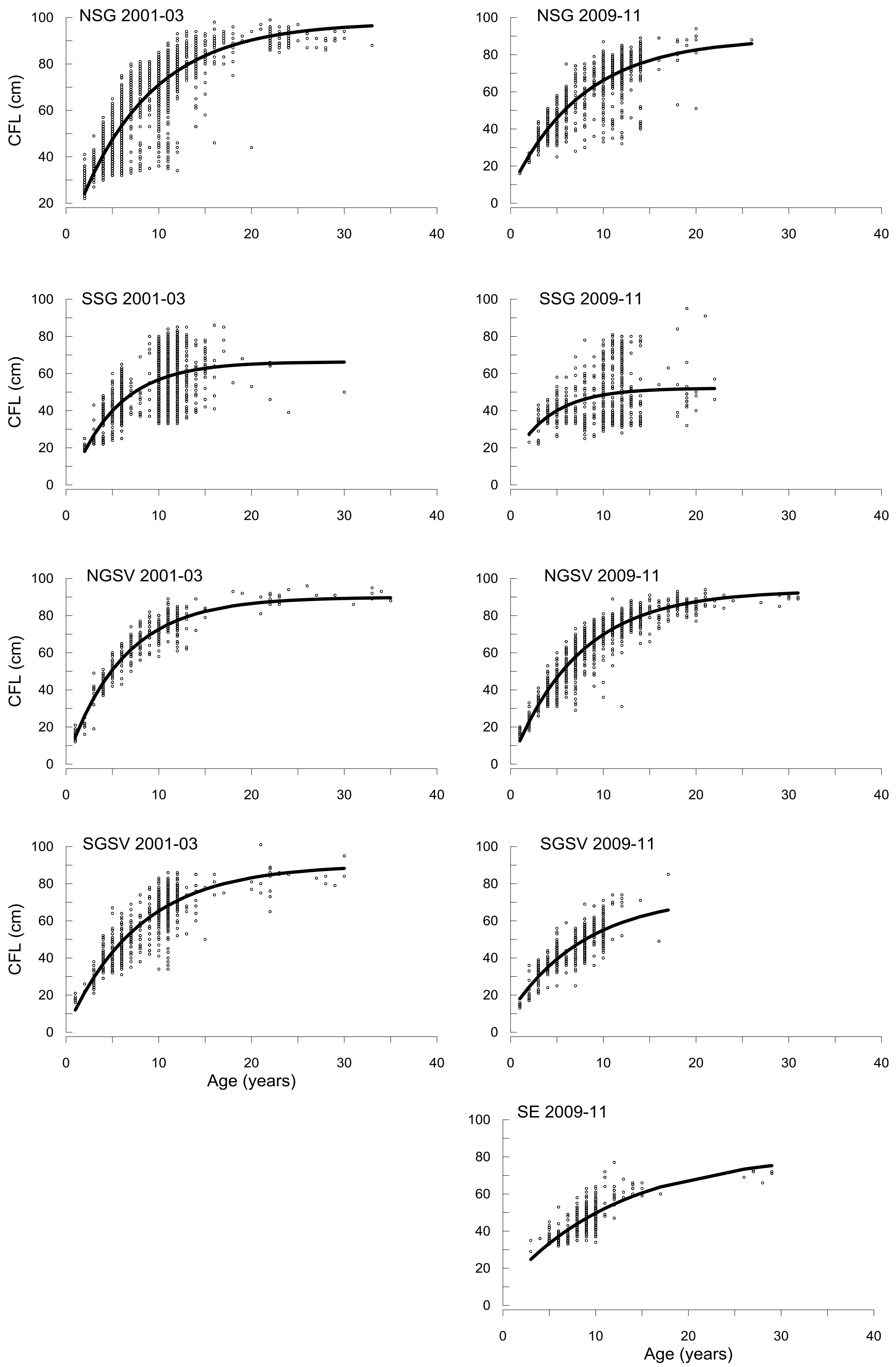

Fig. 2.7 Size-at-age data and von Bertalanffy growth curves for the five regions for the two periods of 2001 to 2003 and 2009 to 2011. Estimates of parameters for growth curves are presented in Table 2.1.

Table 2.1 Estimates of von Bertalanffy growth parameters for the five regions based on estimates of size-at-age for fish sampled in 2001 - 2003 and 2009 - 2011. Estimates of standard errors are shown in brackets.

	2001-03			2009-11		
Region	L_∞	K	t_0	L_∞	K	t_0
NSG	97.9 (1.05)	0.13 (0.004)	-0.27 (0.086)	88.9 (2.92)	0.13 (0.013)	-0.66 (0.292)
SSG	66.3 (1.71)	0.20 (0.023)	0.42 (0.325)	52.1 (2.11)	0.24 (0.083)	-1.14 (1.542)
NGSV	89.9 (1.05)	0.16 (0.006)	-0.09 (0.081)	93.5 (0.95)	0.14 (0.004)	-0.05 (0.093)
SGSV	90.2 (2.29)	0.13 (0.009)	-0.12 (0.220)	74.0 (4.52)	0.12 (0.017)	-1.32 (0.323)
SE	-	-	-	82.2 (4.34)	0.08 (0.011)	-1.40 (0.572)

The size-at-age data from 2009 to 2011 also demonstrated regional differences. For NGSV there were numerous large, old fish, whereas NSG primarily involved fish of <15 years of age. For each of SSG, SGSV and the SE, the fish were relatively young. The resulting growth parameters differed considerably between regions and there was no overlap in the 95% confidence ellipses for the estimates of L_∞ and K. NGSV and NSG had the largest L_∞ estimates and similar growth rates (Fig. 2.8b). SGSV and the SE produced lower estimates of L_∞. SSG again produced the lowest estimates of L_∞ and had the broadest 95% confidence ellipses, reflecting the broad range in size-at-age evident for this region (Fig. 2.7).

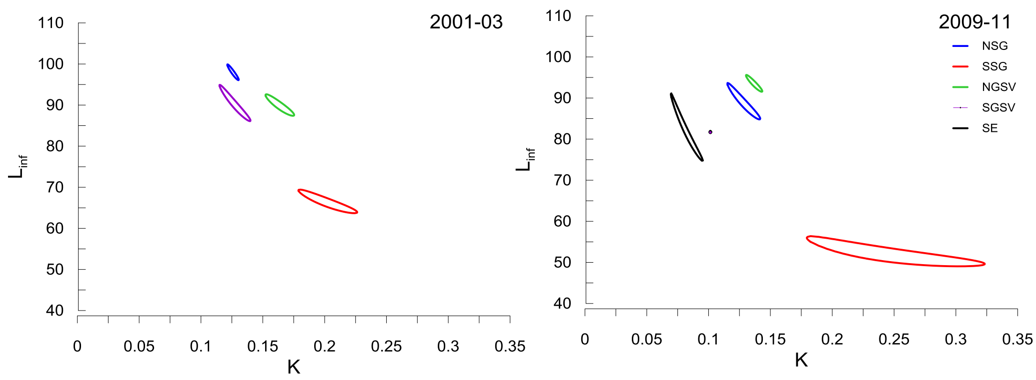

Fig. 2.8 Estimates of 95% confidence limits around the estimated values of the von Bertalanffy growth parameters of K and L_∞, based on measurements of size-at-age from market sampling for snapper from each region. a. 2001 - 2003. b. 2009 - 2011.

2.3.3 Regional recruitment histories

An average recruitment history was calculated for each region based on catch curve analysis from annual age structures. For NSG, the earlier age structures involved considerable numbers of old fish which made it possible to extend the recruitment history back to 1968 (Fig. 2.9). A number of strong year classes are apparent; 1973, 1979, 1991, 1997 and 1999. The 1970s was a period of high recruitment compared to the 1980s that produced exceptionally poor recruitment. Year class strength was highly variable through the 1990s, with exceptional year classes evident in 1991, 1997 and 1999. In comparison, the 2000s had relatively poor recruitment. The last strong year class that recruited to this region prior to 2008 was in 1999. For SSG, the recruitment history did not extend back as far as for NSG as there were fewer older fish captured in this region. Nevertheless, it was again evident that the 1980s was a period of poor recruitment prior to the highly variable recruitment through the 1990s with strong year classes in 1991, 1997 and 1999. No strong year classes are evident after 1999.

For NGSV, the average recruitment history was limited to the period of 1986 to 2008, because of the limited number of annual age structures available (Fig. 2.9). Three years, (1991, 1997 and 1999) produced the strongest year classes. However, the 2001, 2004 and 2006 year classes were also relatively stronger than for the other four regions. For SGSV, the 1980s was also a period of poor recruitment, whilst subsequently the recruitment history was dominated by two particularly strong year classes. The 1991 year class was dominant during the 1990s, whilst the 2001 year class was the dominant one in the 2000s. The 1997, 2004 and 2006 year classes were moderate for this region. For the SE, the estimated recruitment history only extended back to the mid-1990s because of the limited historical catches. It is clearly dominated by the strong 2001 and 2004 year classes.

The recruitment histories of the four gulf regions, (NSG, SSG, NGSV and SGSV) were compared using correlation analysis for the 21 year history of 1986 to 2006. All were significantly correlated (Table 2.2), indicating considerable spatial consistency in the timing of the strong year classes. Nevertheless, it is clear that the relative sizes of the strong year classes varied amongst regions (Fig. 2.9). The recruitment histories of NSG and SSG were most strongly correlated, with both dominated by the strong 1991, 1997 and 1999 year classes. The recruitment history for SGSV was least correlated with the other three regions, possibly relating to the dramatic change in the age structures of this region between the early and latter 2000s.

Table 2.2 Results of correlation analyses between recruitment histories for the four gulf regions between 1986 and 2006. Data shown are the correlation coefficients (** significant at the 0.01 level of significance). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

Region	NSG	SSG	NGSV	SGSV
NSG	1			
SSG	0.8920**	1		
NGSV	0.7196**	0.6853**	1	
SGSV	0.5672**	0.5559**	0.6393**	1

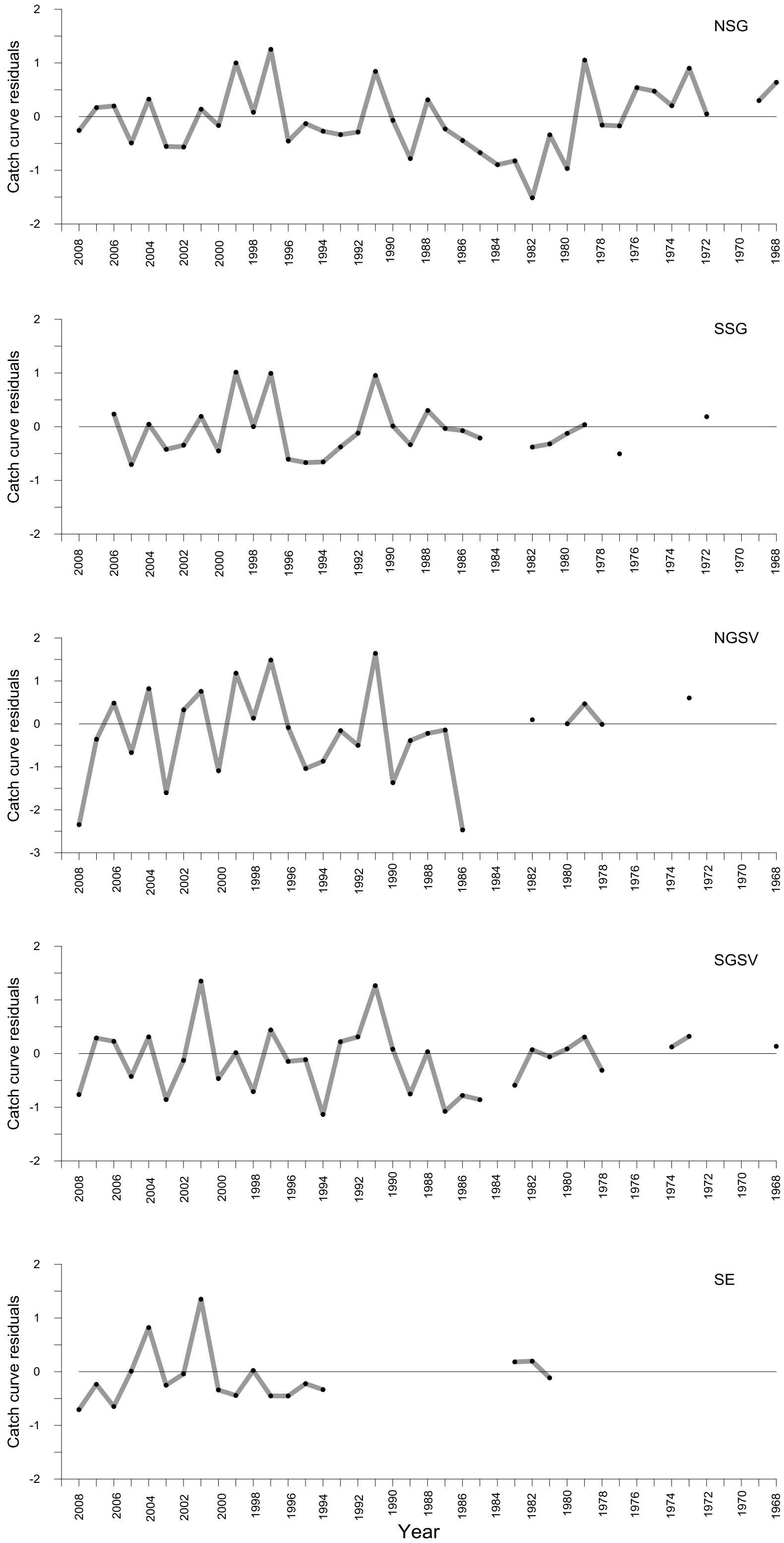

Fig. 2.9 Estimated recruitment histories for five South Australian regions, showing relative year class strength estimated as the average residuals calculated from catch curve analysis from annual age structures determined from market sampling. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

2.4 Discussion

2.4.1 Regional comparisons

The determination of stock structure for a fishery species is a complex process that requires the application of multiple approaches and assessment of possible diverse findings (Begg and Waldman 1999, Baldwin et al. 2012). Towards this end for snapper in SA, the fishery catches and demographic characteristics were compared amongst five regional populations. The basis of this was that if regional populations displayed similar trends in fishery productivity and demographic characteristics then this would support the hypothesis that there was sufficient movement of individuals between them to constitute a single stock. Alternatively, different regional characteristics would be consistent with separate stocks. This regional comparison of catches and demographic information was the first empirical approach towards developing several datasets to be considered in subsequent chapters of this report, which in combination, are to be interpreted in terms of movement and stock structure of snapper in SA.

Inter-regional movement by fish would most likely occur between adjacent regional populations. As such, the comparisons considered here focus at this scale. NSG and SSG were historically the most productive regions in SA's snapper fishery. However, since 2008, their catches declined to their lowest levels. Both populations had similar age structures that resulted in highly correlated recruitment histories. Such similarities suggest the influence of shared demographic processes at the regional scale. Nevertheless, there were also important differences between them. The regional size structures through both periods differed considerably, which related most strongly to regional differences in growth patterns, but also to subtle differences in age structures. Many fish from SSG had slower growth, did not attain the same size-at-age or asymptotic size and so were smaller for their ages than those from NSG and elsewhere. The persistence of such fish in SSG, but their rarity elsewhere, indicates some separation amongst regions, suggesting relatively restricted movement patterns.

For NGSV and SGSV in 2001-03, the fishery catches, and population size and age structures were quite similar. The regional catches were low and dominated by 'large' fish predominantly from the 1991 year class, augmented with a few smaller ones mainly from the 1997 and later the 1999 year classes. Such similarities between regions changed profoundly from 2008 onwards. From this time, annual catches from NGSV increased exponentially to a record level in only a few years and the population had a broad size range that included many 'large' and 'very large' fish, reflecting numerous strong year classes from 1991, 1997, 1999, 2001, 2004 and 2006. This meant that from 2009 to 2011, many fish from the 3+ to 20+ age classes contributed to the population. In comparison, the fish from SGSV were much smaller, grew more slowly, had a lower asymptotic size and mostly came from the exceptional 2001 year class, augmented by the 2004 and 2006 year classes.

The regional comparisons presented above identified some similarities between adjacent regional populations in the temporal dynamics of fishery productivity and population characteristics, but also some important differences. The fact that such differences can persist over a number of years means that the adjacent populations are not fully inter-mixed. Rather, the differences indicate that at least some fish that occupy different regions must have occupied different water masses for significant parts of their lives. This observation is consistent with fish originating in the northern nursery grounds, of which some subsequently moved to the southern regions. The similarities in age structures between NSG and SSG and also between NGSV and SGSV during 2001 to 2003 are consistent with this, as more fish from the stronger year classes would be expected to move from the north to the south. The different growth patterns evident for the southern regions indicate that at least some fish that moved south then remained in these regions subsequently growing more slowly than those that remained in the north. However, the presence of some large fish in the southern gulfs is consistent with some fish mixing between the northern and southern gulfs.

The comparison of population characteristics between NGSV and SGSV for 2009 to 2011 gave very different results. Whilst it is not possible to discount that the fish that inhabited SGSV through this period originated in NGSV, the differences in regional age structures and growth patterns suggest very little subsequent inter-regional movement, implying regional separation through this period. Alternatively, at this time, there were considerable similarities between the populations of SGSV and the SE suggesting intermixing between these populations. This raises the question about the regions of origin of the high fishable biomass that was evident in the SE from 2008 to 2012. Did these fish originate from one or both of the northern gulfs, did they originate from nursery areas in local bays of the SE region or is it possible that they originated in Port Phillip Bay, i.e. the main spawning ground and nursery area for the Western Victorian Stock (Hamer et al. 2005, 2006, 2011)?

2.4.2 Conclusions

There were considerable changes in the spatial structure of SA's snapper fishery between the earlier and latter 2000s. The demographic processes responsible for these changes were not understood reflecting our poor understanding of large-scale movement patterns and their implications for stock structure. These issues were addressed through comparisons of regional demographic characteristics. There were considerable spatial and temporal similarities and differences that provided some insight into fish movement and stock structure. For NSG and SSG, similarities in demographic characteristics suggested that the former was a possible source population for the latter. Also, similarities between the SGSV population from 2001-03 to the two northern gulf populations suggested that they were possible source populations. However, the population characteristics for SGSV from 2009-11 were different from the other gulf populations, but similar to those of the SE population. This suggests that there may have been considerable interchange between these two regional populations and a possible shared, but unknown origin.

The issues about the regions of origin of fish and their subsequent movements are considered in the following chapters of this report, based on the regional analysis of the chronological structure and chemistry of otoliths.

3. Physical characteristics of otoliths

Anthony Fowler, Michael Steer

3.1 Introduction

Determining the stock structure for a fishery species identifies the spatial scale at which populations are essentially self-sustaining thereby pointing to the appropriate scale at which fishery management should be applied (Bailey 1997, Begg and Waldman 1999). Managing a fishery at a spatial scale that does not recognise the true complexity of the sub-structure of populations may lead to localised depletion from which subsequent recovery can take considerable time (Bailey 1997). However, determining the stock structure for a species is challenging as it ultimately depends on the scale of movement of individuals at all stages throughout the life history. Given the challenges of understanding fish movement in marine environments, inferences about stock structure are often based on comparing phenotypic and genotypic characteristics of individual fish between different populations (Pawson and Jennings 1993).

Analysis of otoliths can contribute to understanding stock structure. Otoliths grow through the accretion of new crystalline and organic matrix material to their growing surfaces (Campana 1999), culminating in annual increments consisting of opaque and translucent zones (Campana and Thorrold 2001, Fowler 2009). They are metabolically inert, as they are not subsequently reworked, as occurs with skeletal material of vertebrates (Campana and Neilson 1985). Their chemistry also varies regionally, reflecting environmental variation (Campana 1999, Fowler 2009, Kerr and Campana 2014). Therefore, the sequential nature of otolith deposition, its incremental structure, the fact that such deposition is environmentally-mediated, and the otolith material is subsequently not altered metabolically means that otoliths retain a chronological record of the environments that the fish has experienced throughout its life (Campana 1999, Panfili et al. 2002).

A transverse section of an otolith exposes the crystalline structure of the chronological layers deposited throughout the fish's lifetime. This allows age-related information in the otolith structure such as the increment widths, optical density and chemistry to be compared amongst regions and hypotheses to be addressed about past environments occupied. Such hypotheses may relate to whether fish sampled as adults from different regions originated from the same nursery area, and when significant movement occurred that resulted in separation into different regional populations.

Otoliths of adult snapper from regional waters of South Australia (SA) display annual increments that reflect fish age in years (McGlennon et al. 2000, Fowler and McGlennon 2011, Fowler et al. 2013). However, there is considerable variation in the physical characteristics of snapper otoliths – some display greater contrast between the opaque and translucent zones which allows their structure to be interpreted more confidently than less clear otoliths (Fowler et al. 2004). If such physical characteristics are environmentally-mediated, then it is possible that otoliths can contribute to retrospectively determining where fish originated and their subsequent large-scale, inter-regional movements. Inferences about stock structure can be drawn from such observations (Fowler et al. 2004).

The primary aim of this chapter was to compare the physical characteristics of otoliths from different regions of South Australian waters, to consider their contribution to determining the stock structure. Two sets of variables were assessed. The first were single measurements such as otolith and fish size at the time of fish capture. Regional differences in such characteristics would indicate the likelihood that fish from different regions had occupied different marine environments for considerable periods of time. The second set of variables were measured across the chronological structure of the otoliths and thereby provided age-related information, to address hypotheses such as where fish originated and when they may have undertaken migration.

3.2 Methods

3.2.1 Sample collection

The physical characteristics measured from the transverse (TS) sections of snapper otoliths were: size; increment widths; interpretability; and opacity. Appropriate parameters were measured from transverse sections of otoliths and compared amongst five South Australian regions, i.e. Northern Spencer Gulf (NSG), Southern Spencer Gulf (SSG), Northern Gulf St. Vincent (NGSV), Southern Gulf St. Vincent (SGSV) and the South East (SE). Some inter-regional comparisons also involved fish from Port Phillip Bay (PPB) in Victoria. Otoliths from four particular year classes were considered, (i.e. 1991, 1997, 2001 and 2004), which had previously been recognised as strong year classes in some regions (Chapter 2 this report, Fowler et al. 2013), providing the best chance of there being sufficient samples for regional comparisons. The otoliths from each year class were sampled in the same year, which meant that regional comparisons involved fish of the same age that had lived through the same time period, thus minimising the possibility of there being confounding spatial and temporal influences. The otoliths from the different year classes were of different ages (Table 3.1), and so statistical comparisons were done for each year class separately. The sizes of fish in the different year classes and from which the otoliths were removed were also compared amongst regions. Fish size was classified into four size categories, i.e. ‘small’ (30 – 40 cm CFL), ‘medium’ (40 – 60 cm CFL), ‘large’ (60 – 80 cm CFL), and ‘very large’ (>80 cm CFL).

Table 3.1 Information about samples considered in the regional comparison of physical characteristics of snapper otoliths. Data for each year class include: year the otoliths were collected; their age at time of collection; the number of fish from which otoliths were collected for each year class and region; and the number considered in the increment width analysis. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Year class	Year sampled	Fish age (years)	Region	No. collected	No. inc width analysis
1991	2003	12	NSG	249	16
			SSG	199	15
			NGSV	62	15
			SGSV	86	15
1997	2008	11	NSG	143	18
			SSG	239	15
			NGSV	43	16
			SGSV	16	15
2001	2009	8	NSG	30	15
			SSG	25	15
			NGSV	43	15
			SGSV	200	15
			SE	69	13
2004	2009	5	NSG	75	29
			SSG	30	26
			NGSV	29	25
			SGSV	83	35
			SE	13	13

For each year class, approximately 15 otoliths for each region were randomly selected from those available in the library of sectioned otoliths that had resulted from SARDI's long-term market sampling program (Chapter 2 this report, Fowler et al. 2013) (Table 3.1). The otoliths from PPB were provided from the collection developed by Fisheries Victoria.

3.2.2 Processing digital images

Several digital images of each TS-section were recorded using an image analysis system with a Leica MS5 dissecting microscope, Leica DC300 digital camera and Image Pro Plus (Version 7.0, Media Cybernetics, Inc.). First, one image was recorded at x10 magnification after which images of the dorsal and ventral halves of the sectioned otolith were recorded at x16 and x25 magnification. Consistent settings of aperture size, light intensity, mirror position and shutter speed of 0.5 s were used.

Processing the digital images for the collection of data was also done with Image Pro Plus. The multiple images of the otolith were assessed to ensure that the correct estimate of age had originally been assigned. If not, it was discarded and replaced by another randomly selected TS-section. If the correct age had been assigned, the image at x10 magnification was used to measure the major axes from the otolith core to the furthest points (Axes II, III, and V) (Fig. 3.1a). Measurements for Axis I were not considered as they were difficult to interpret because for many otoliths this axis was curved, and for some there was a calcareous abnormality located at the ventral tip, which complicated determining its end point. Axis IV also was not measured as there was no obvious end point to measure to. The ratios of Axis II : Axis V and Axis III : Axis V were calculated to consider the relative growth rates along both axes.

The images of the dorsal and ventral halves of the otolith taken at higher levels of magnification were then examined to compare the interpretability of the increment structure along each of Axes II, III, IV and V. The macrostructure along each axis was assigned a grade from 1 to 4 (1 – increment structure uninterpretable; 2 – increment structure poor, moderate level of confidence in interpretation; 3 – increment structure clear, high level of confidence; 4 - increment structure very clear, very high level of confidence). Then, the widths of the individual increments were measured along two axes, i.e. Axis V from the core to the dorsal edge and Axis II located on the ventral side of the sulcus (Fig. 3.1b). Measurements were made from increment to increment, perpendicular to the increment structure, starting from the core and progressing to the outer edge along the path of maximum growth.

Optical density is inversely related to the amount of light that is transmitted through material and therefore is representative of its translucence (Anon 2009). For each otolith from the 2001 and 2004 year classes, the image of its dorsal half recorded at x25 magnification was used to measure the annual estimates of optical density across the otolith along Axis V (Fig. 3.1c). The coloured digital image was first converted to a Gray Scale 8 bit image. Then a small square 'area of interest' was created and placed over the first opaque zone, and the 'Measure – histogram' function was used to calculate the average optical density of the pixels represented in the 'area of interest' (Fig. 3.1c). The small 'area of interest' was then placed, in turn, over each subsequent opaque zone and the average optical density of all pixels in the 'area of interest' was recorded. Finally, the 'area of interest' was moved across the section following Axis V, systematically changing its shape to fit into each translucent zone and recording the optical density. Specific placing of the 'area of interest' tried to avoid discontinuities and artefacts in the otolith structure to provide, as far as possible, genuine contrast between the opaque and translucent zones. For the otoliths from the 2001 year class, this process provided 16 consecutive estimates of optical density, i.e. eight recorded in the opaque zones and eight in the translucent zones. For the fish from the 2004 year class there were 10 consecutive estimates of optical density, i.e. five for the opaque zones and five for the translucent zones.

3.2.3 Data Analyses

The regional comparisons of data were undertaken with a combination of univariate and multivariate analyses, using SPSS Statistics (Version 22). For each year class, the measurements of fish size and of the sizes of the major axes of the TS-sections were compared amongst regions using single factor analyses of variance (ANOVA). Prior to each test, the data were tested for homogeneity of variances using Levene's Test. When heterogeneous variances were identified the data were transformed appropriately and reconsidered. When an ANOVA identified a significant regional difference, *a posteriori* comparisons were done using a Student-Newman-Keuls test to identify the differences amongst regional means.

The cross-otolith increment width data were analysed independently for each of Axis V and Axis II for each year class. In each case, a split-plot repeated measures ANOVA was done for which the within-subjects variable was increment number, the between subjects variable was region and the dependent variable was increment width. The various assumptions for this statistical procedure were tested for each data set which involved: Levene's Test of Equality of Error Variances; Mauchly's Test for Sphericity; and Box's M Test for the Equality of Covariance Matrices. Where the data had heterogeneous variances, they were transformed using $\log_{10}(x + 1)$. Mauchly's Test for Sphericity was violated for every analysis, so the Huynh and Feldt correction was used to adjust F-critical values to protect against inflated Type 1 errors in the repeated measures ANOVAs. The results of these were compared with repeated measures MANOVAs to ensure that outcomes were reliable.

The results for the classification of otoliths with respect to their readability and interpretability for each year class were compared amongst regions using chi-squared contingency tests. Each analysis tested the null hypothesis that the proportions of the assigned grades did not differ between regions.

The optical density data for the 2001 and 2004 year classes were first analysed using split-plot repeated measures analyses of variance. Two such analyses were done for each year class, i.e. one for the measurements from the opaque zones and one for the translucent zones across the otolith sections (Fig. 3.1c). The within-subjects variable was increment number, the between-subjects variable was region, and the dependent variable was optical density as recorded either in the translucent or opaque zones. Prior to each statistical analysis, the appropriate assumptions were tested as for the increment width data. The optical density data were then compared amongst regions using a series of multivariate analyses of variance (MANOVA), one for each annual increment across the otolith. The two dependent variables considered for each increment number were the optical density measures for the translucent and opaque zones. Prior to each analysis the data were assessed for conforming to the assumptions of the analysis using Levene's test for the equality of variances and Box's M test for the equality of covariance matrices.

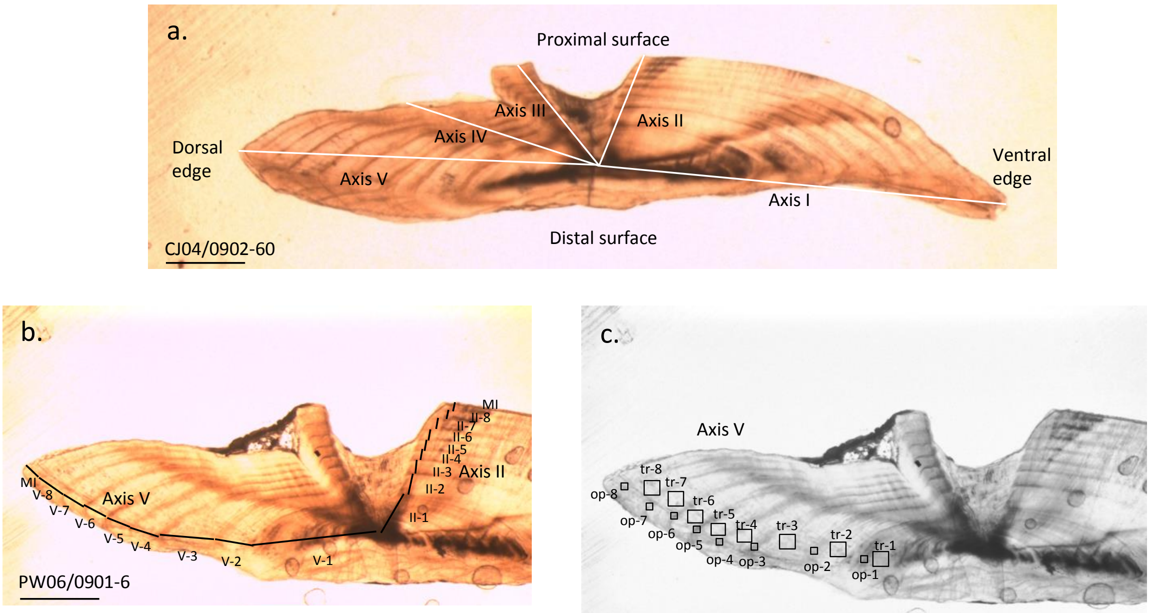

Fig. 3.1 Digital images of TS-sections of otoliths showing measurements recorded. a. Major axes measured on each TS-section. b. Increment measurements recorded along Axes V and II for each TS-section. c. Gray scale, 8 bit image of TS-section showing where optical density was measured for opaque and translucent zones along Axis V. Scale bars = 1000 µm.

3.3 Results

3.3.1 1991 Year Class

Regional Comparison of Fish Sizes

Through market sampling in SA in 2003, a total of 596 otoliths were collected from the 1991 year class of snapper for which there was an uneven contribution from the different regions (Table 3.1). A total of 75% of these otoliths came from NSG and SSG, with the remainder from NGSV and SGSV, and none from the SE. The regional size distributions of the 12+ fish from which the otoliths were removed were unimodal for each of NSG, NGSV and SGSV, were similar between regions and predominantly involved ‘large’ fish (Fig. 3.2). However, the size distribution for fish from SSG was multi-modal, involved ‘large’ fish but also several modes of ‘small’ and ‘medium’ fish that were small for their age relative to the other regions.

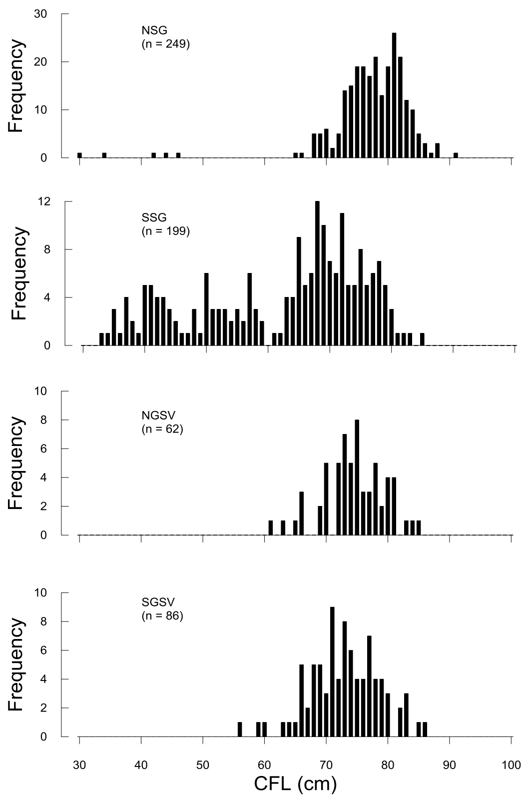

Fig. 3.2 Size frequency distributions of snapper from the 1991 year class that were sampled in 2003 from the four South Australian regions. CFL – caudal fork length, NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Spencer Gulf.

The sizes of the 61 fish whose otoliths were considered in the increment width analysis (Table 3.1) were compared amongst regions. The ANOVA indicated a significant difference amongst regions with the mean size of fish from SSG, smaller than those from the other four regions (Fig. 3.3). However, the analysis result is complicated by the fact that the data had intractably heterogeneous variances, which related to the high variation in the sizes of fish from SSG.

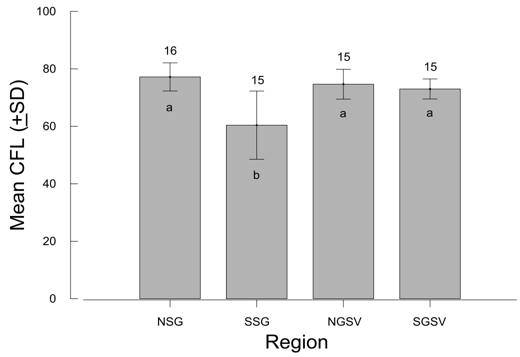

Fig. 3.3 Average size (cm) of snapper from the 1991 year class from the four regions whose otoliths were considered in the increment width analysis. Sample sizes are indicated above error bars and results from Student-Newman-Keuls test are indicated as pronumerals below error bars (means with the same pronumeral are not significantly different). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

Regional Comparison of Otolith Characteristics

Major Axis Measurements

For each of the major axis measurements as well as the ratios, a single factor ANOVA compared the results amongst regions (Fig. 3.4). In each case, the data were not transformed as the variances were homogeneous. Only for Axis II was there a marginal regional difference for which the post hoc comparison indicated that the otoliths from NSG were marginally larger than those from SSG (Fig. 3.4). In general, the otoliths from the four regions were similar in size and had similar ratio estimates.

Increment Width Analysis

Otoliths from the 1991 year class sampled in 2003 had 12 complete opaque zones that were measured along Axes V and II. For the four regions, the increment widths declined exponentially from V-1 to V-12 along Axis V, and from II-1 to II-12 along Axis II, from the centre towards the otolith edge (Fig. 3.5). The split-plot repeated measures ANOVA for Axis V had a significant interaction between regions and years, which meant that the pattern of decline in increment widths from V-1 to V-12 varied amongst regions. The regional estimates of increment widths were similar for V-1, V-2 and V-3, and then diverged from V-4 onwards, with the greatest difference amongst regions evident for V-5 to V-9. Subsequently, the increment widths reconverged (Fig. 3.5a). For Axis II, the data demonstrated the same patterns as for Axis V, i.e. the measurements for II-1 to II-4 were similar amongst regions, then diverged between II-5 to II-8, before reconverging for II-9 to II-12 (Fig. 3.5b).

Transverse sections of some otoliths from the 1991 year class sampled in PPB were also available for comparison of increment width trajectories with those from the South Australian regions. The PPB fish were sampled in 2000, which meant their otoliths did not fully overlap with those from South Australia, and so were excluded from the analyses presented above. However, as the otolith structure did overlap for the years of 1991 to 1999, they were compared for those years. The repeated measures ANOVAs for the two axes both gave significant interactions between regions and years. The V-1 and II-1 measurements for the PPB otoliths were much broader than those from the SA regions, presenting a strong difference in the patterns of growth between the Victorian and South Australian otoliths (Fig. 3.6).

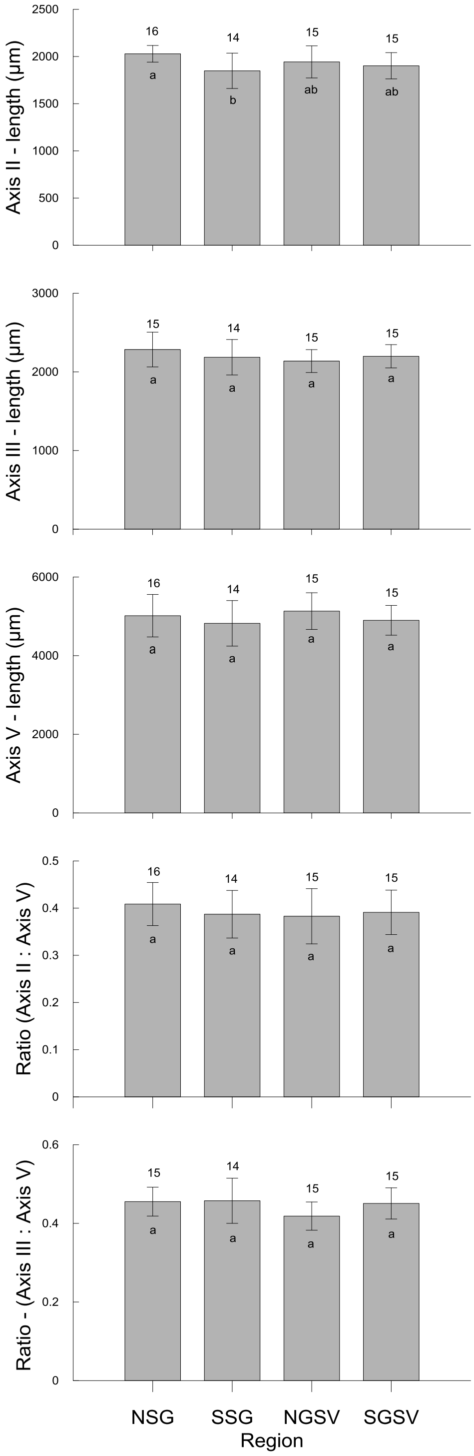

Fig. 3.4 Regional comparisons of mean (±SD) axis measurements and ratios of measurements from TS-sections of otoliths from the 1991 year class for the four South Australian regions. The sample sizes are indicated above error bars and results from Student-Newman-Keuls tests are indicated by pronumerals below error bars. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

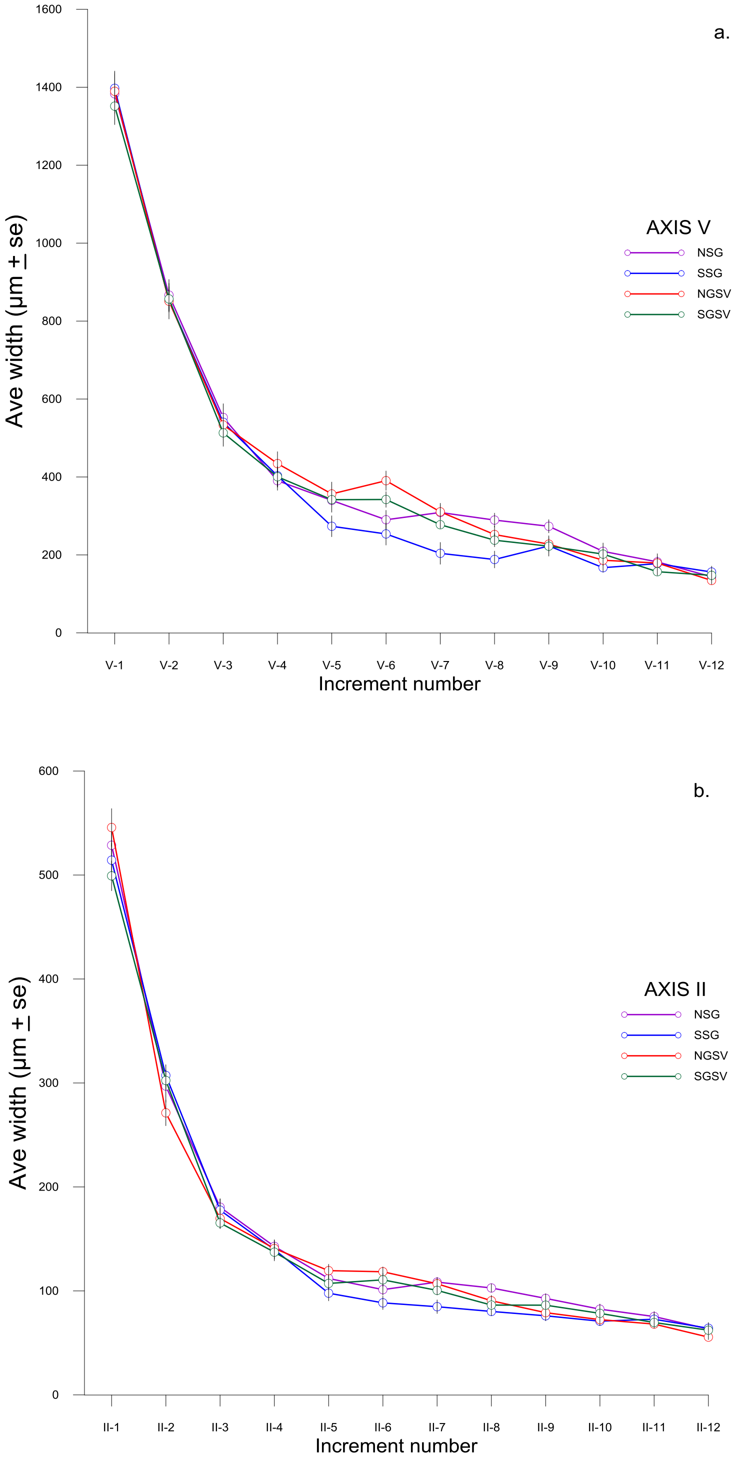

Fig. 3.5 Regional comparison of average increment widths across otoliths from the 1991 year class from the centre to the edge along Axes V and II for the four South Australian regions (for location of axes in the TS-section refer to Fig. 3.1). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

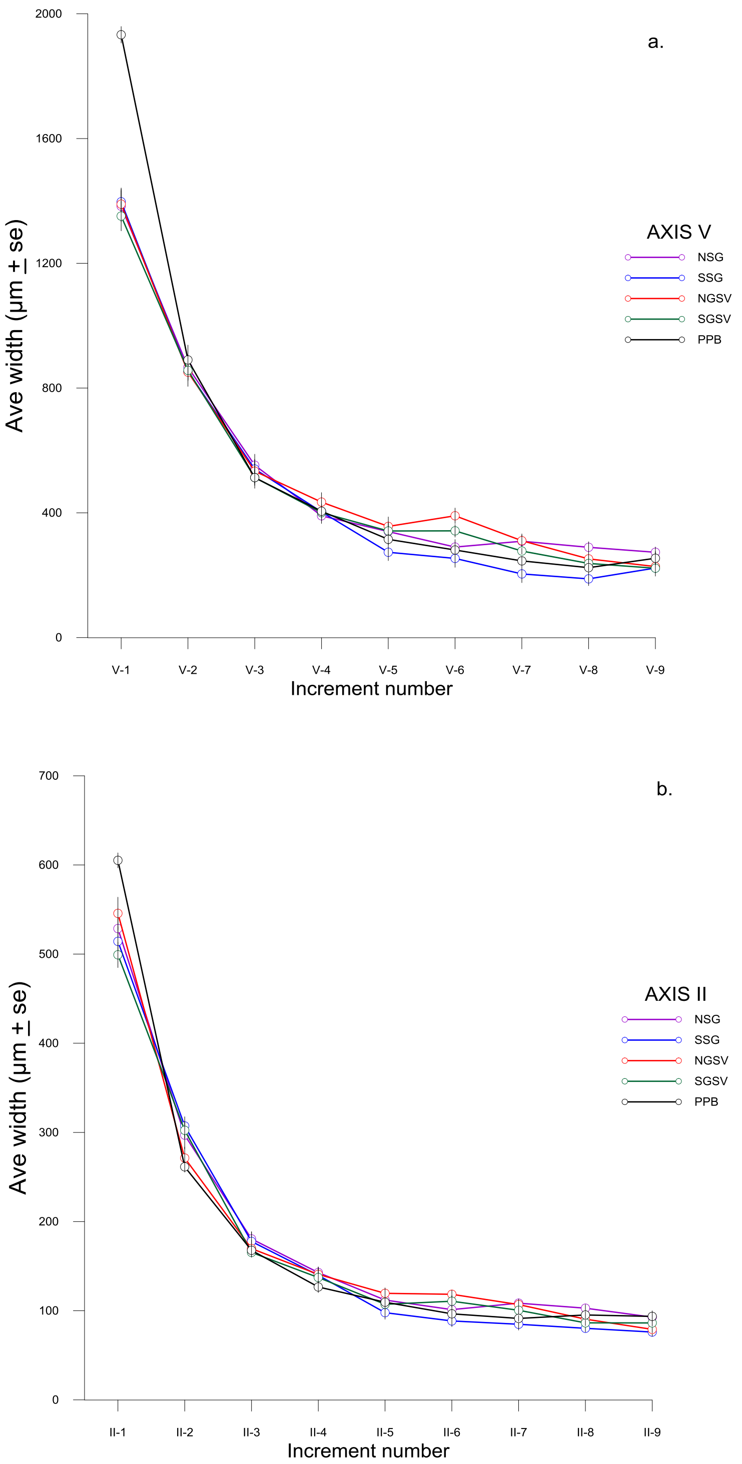

Fig. 3.6 Regional comparison of average increment widths across otoliths from the 1991 year class from the centre to the edge along Axes V and II for four South Australian regions and Port Phillip Bay, Victoria (for location of axes in the TS-section refer to Fig. 3.1). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, PPB – Port Phillip Bay.

Classification of Otolith Clarity

The four axes (Axes II-V) were assigned a grade as a qualitative measure of the clarity of the incremental structure and confidence in the age estimate (Fig. 3.7). For each axis, the chi-squared test indicated that the grades differed significantly amongst regions (Axis II – X^2 = 18.1, df = 6, $p < 0.01$; Axis III – X^2 = 15.4, df = 6; $0.01<p<0.025$; Axis III – X^2= 18.1, df = 9, $0.025<p<0.05$; Axis V – X^2 = 19.0, df = 6, $p < 0.005$). Within each gulf, the northern region had more otoliths assigned higher grades than the respective southern region. Also, more otoliths from Spencer Gulf were assigned Grades 3 and 4 than those from Gulf St. Vincent. These data suggest two levels of spatial differentiation in otolith clarity, i.e. between gulfs, and between the north and south regions of the two gulfs.

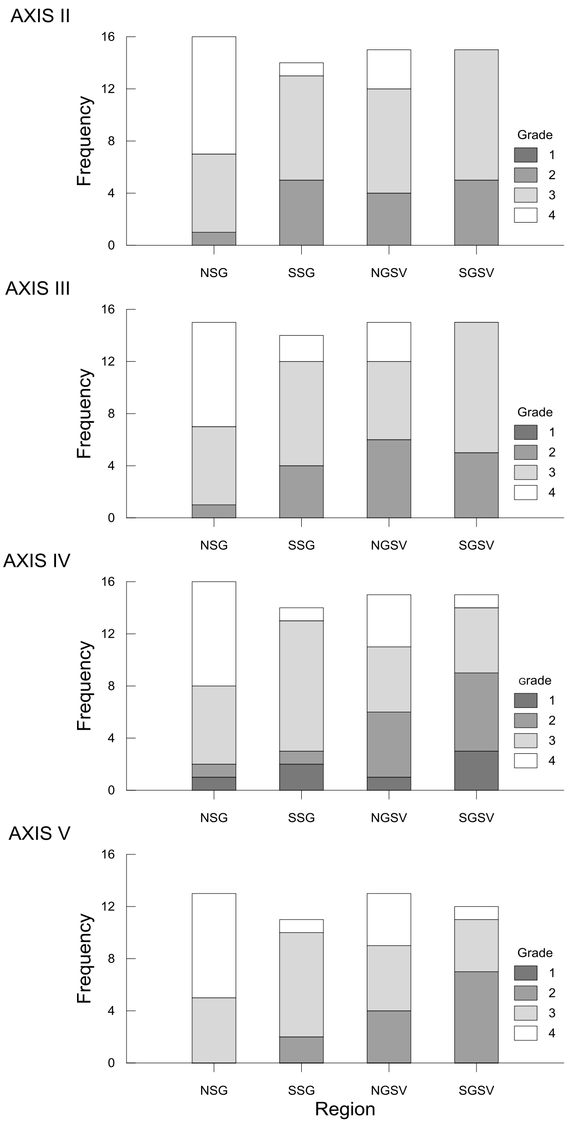

Fig. 3.7 Results from the classification of clarity for Axes II to V for otoliths from the 1991 year class sampled from different regions. Grades: 1 – cannot interpret; 2 – poor; 3 – good; 4 – excellent. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

3.3.2 1997 Year Class

Regional Comparison of Fish Sizes

A total of 441 otoliths were collected from fish from the 11+ year class in 2008 (Table 3.1). The contribution from the different regions was uneven, with 86.6% of otoliths from NSG and SSG, the remainder from NGSV and SGSV, and none from the SE (Fig. 3.8). The regional size frequency distributions of the fish from which otoliths were collected were unimodal for NGSV and NSG, and primarily involved 'large' fish (Fig. 3.8). In contrast, the size distribution for fish from SSG was skewed to the left as there was a considerable number of small fish. Otoliths were collected from only 16 fish from SGSV.

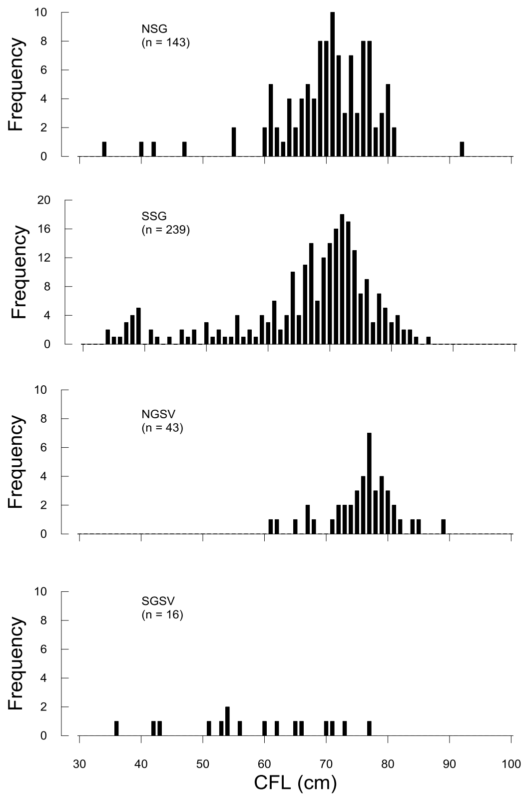

Fig. 3.8 Size frequency distributions of snapper from the 1997 year class that were sampled in 2008 from the four South Australian regions. CFL – caudal fork length, NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

The sizes of the 64 fish whose otoliths were considered for increment width analysis were compared using a one factor analysis of variance. Whilst the analysis indicated a significant difference amongst regions, the data had intractably heterogeneous variances. This related to the broad ranges of fish size from each of SSG and SGSV for which there were more small fish than in the respective northern regions (Fig. 3.9).

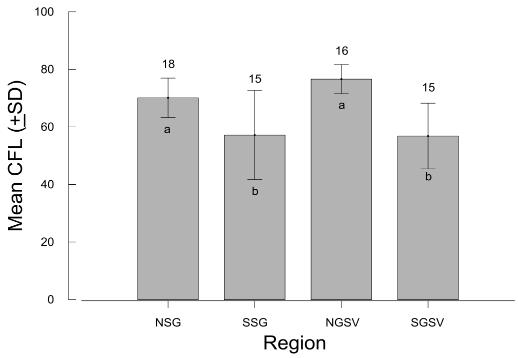

Fig. 3.9 Average size (cm) of snapper from the 1997 year class whose otoliths were considered in the increment width analysis. Sample sizes are indicated above the error bars and results from Student-Newman-Keuls tests are indicated as pronumerals below the error bars. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

Regional Comparison of Otolith Characteristics

Major Axis Measurements

The regional differences in fish size were manifested in the comparisons of major axes measurements of the otoliths (Fig. 3.10). Those from NGSV and NSG were significantly larger along Axes III and V than those from SSG and SGSV. There were no differences in the ratios of Axis II : Axis V and Axis III : Axis V.

Increment Width Analysis

The otoliths from the 1997 year class had 11 complete opaque zones. The measurements of increment widths along Axes V and II declined exponentially (Fig. 3.11). The repeated measures ANOVA for each axis had a significant interaction, indicating that both patterns of exponential decline varied amongst regions. For Axis V, there was little difference amongst regions in the widths of V-1, V-2 and V-3. Then for each of V-4, V-5, V-6 and V-7 there was considerable separation amongst regions with differences in widths greatest between fish from NGSV and SSG, with intermediate levels for NSG and SGSV. The results for Axis II were very similar.

Otoliths from PPB were also considered in a regional increment width comparison. The PPB fish were sampled in 2005, which meant that there were seven complete annual increments whose widths overlapped with those from the South Australian regions. The repeated measures ANOVAs for Axes V and II demonstrated significant interactions, indicating that the patterns of decline in increment widths varied amongst regions. The fish from PPB had the broadest widths for V-1 and II-1, which dropped to near the lowest values for V-2, V-3 as well as II-2 and II-3 (Fig. 3.12). For subsequent increments, the widths were intermediate relative to those of the South Australian regions.

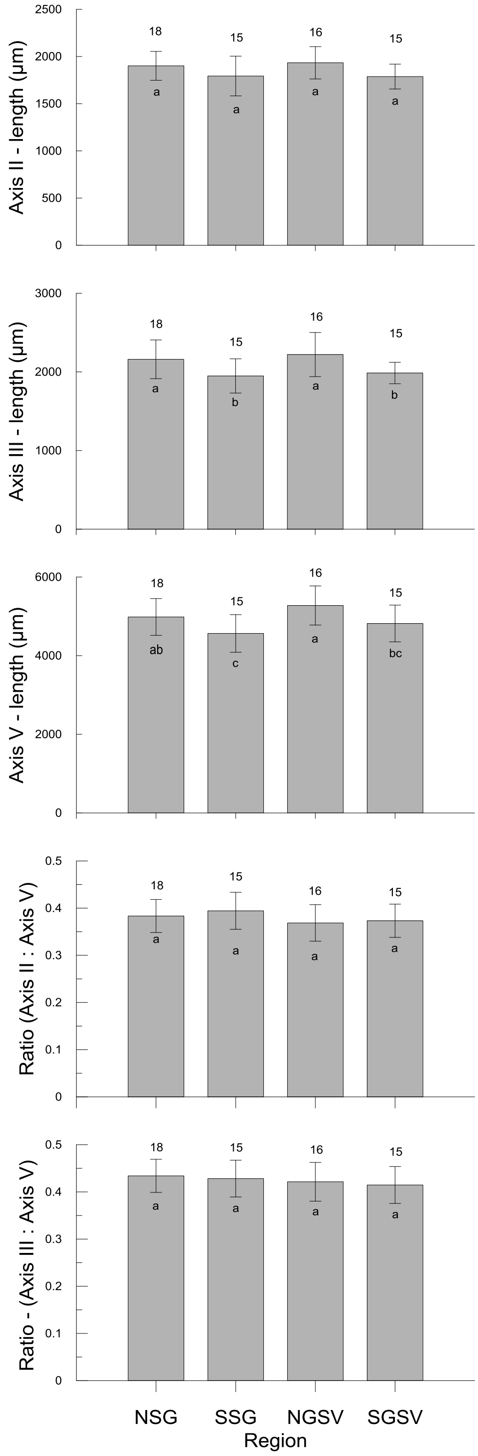

Fig. 3.10 Regional comparisons of mean (±SD) axis measurements and ratios of measurements from TS-sections of otoliths from the 1997 year class for the four South Australian regions. The sample sizes are indicated above error bars and results from Student-Newman-Keuls tests are indicated by pronumerals below error bars. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

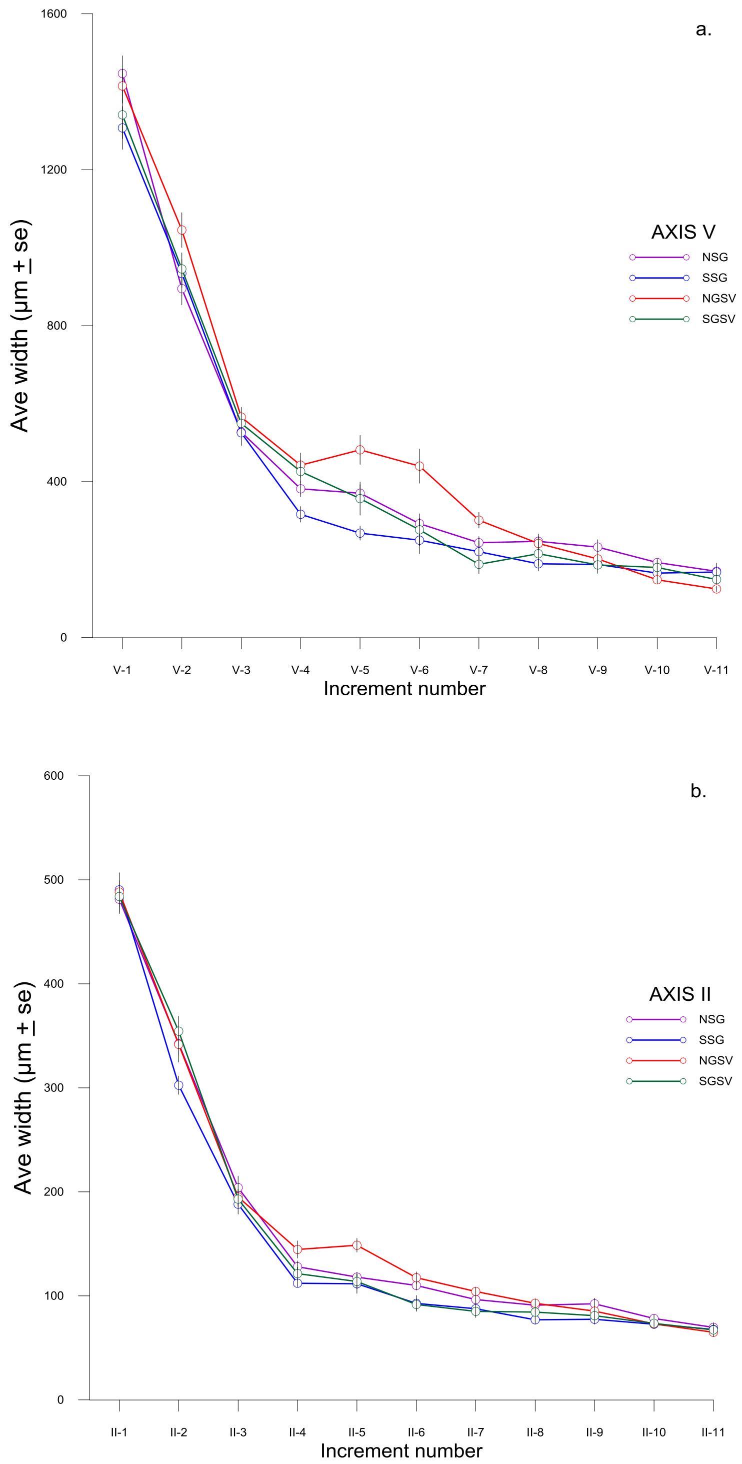

Fig. 3.11 Regional comparison of average increment widths across otoliths from the 1997 year class from the centre to the edge along Axes V and II for the four South Australian regions (for location of axes in the otolith TS-section refer Fig. 3.1). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

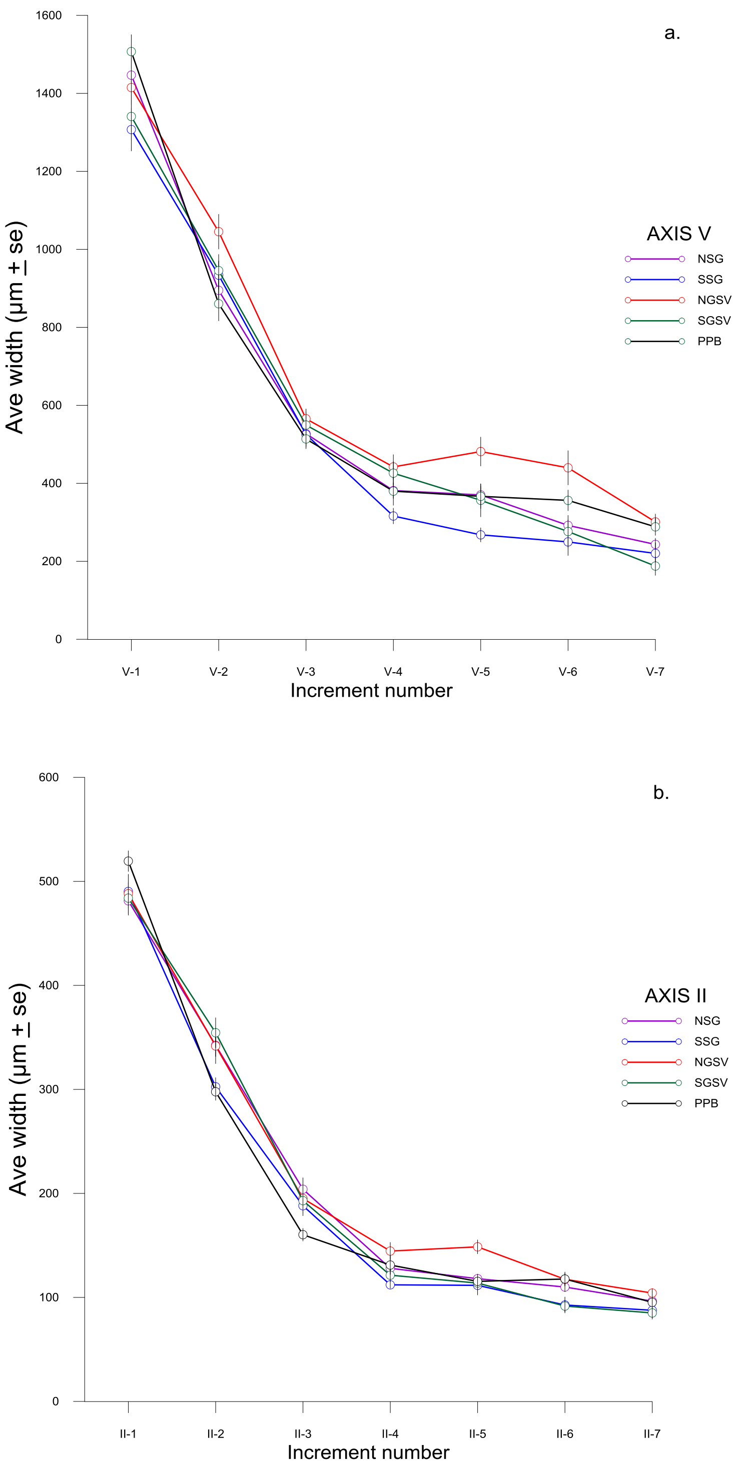

Fig. 3.12 Regional comparison of average increment widths across otoliths from the 1997 year class from the centre to the edge along Axes V and II for four South Australian regions and Port Phillip Bay, Victoria (for location of axes in the otolith TS-section refer Fig. 3.1). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

Classification of Otolith Clarity

The grades of clarity assigned to the otoliths from each of the four South Australian regions were diverse (Fig. 3.13). The chi-squared contingency tests identified no significant differences amongst regions in the proportional assignment of the grades for any of the four axes (Axis II – $X^2 = 7.8$, df = 9, $0.1<p<0.25^{ns}$; Axis III – $X^2 = 13.0$, df = 9, $0.1<p<0.25^{ns}$; Axis IV – $X^2 = 3.6$, df = 9, $0.9<p<0.95^{ns}$; Axis V – $X^2 = 13.7$, df = 9, $0.1<p<0.25^{ns}$). Therefore, for the otoliths from the 1997 year class, inter-regional differentiation in otolith quality was less apparent than for the other three year classes.

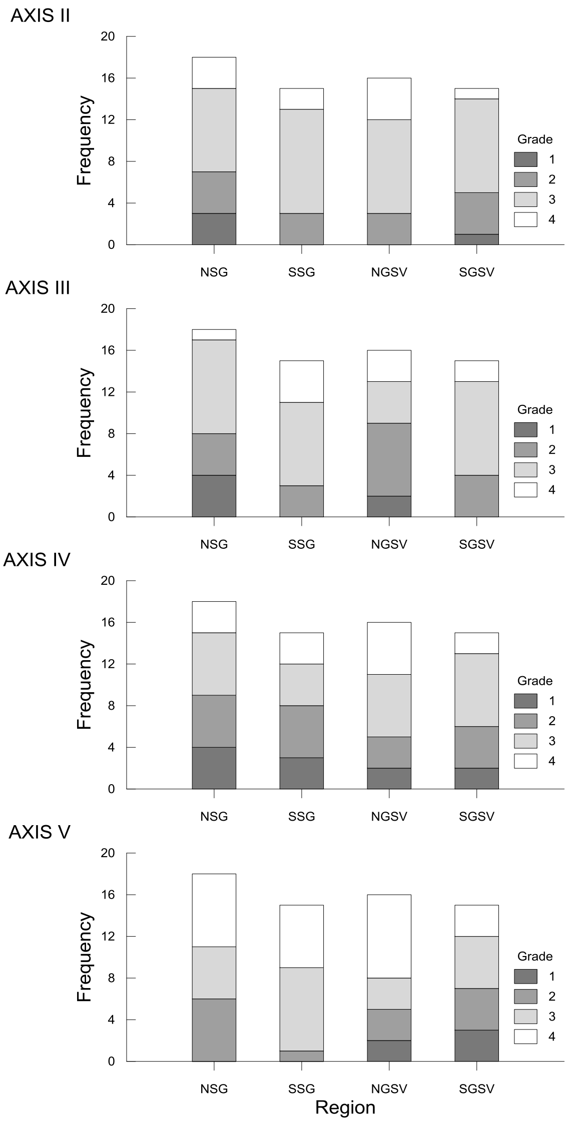

Fig. 3.13 Results from the classification of the four axes (II to V) for otoliths from the 1997 year class sampled from different regions, according to the clarity and interpretability of the otolith structure. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent.

3.3.3 2001 Year Class

Regional Comparison of Fish Sizes

In 2009, otoliths were collected from 367 fish from the 2001 year class that came from five South Australian regions (Table 3.1). More came from Gulf St. Vincent than Spencer Gulf, reflecting changes to the spatial structure of South Australia's snapper fishery (Chapter 1). Furthermore, fish from the SE were included in the regional comparison.

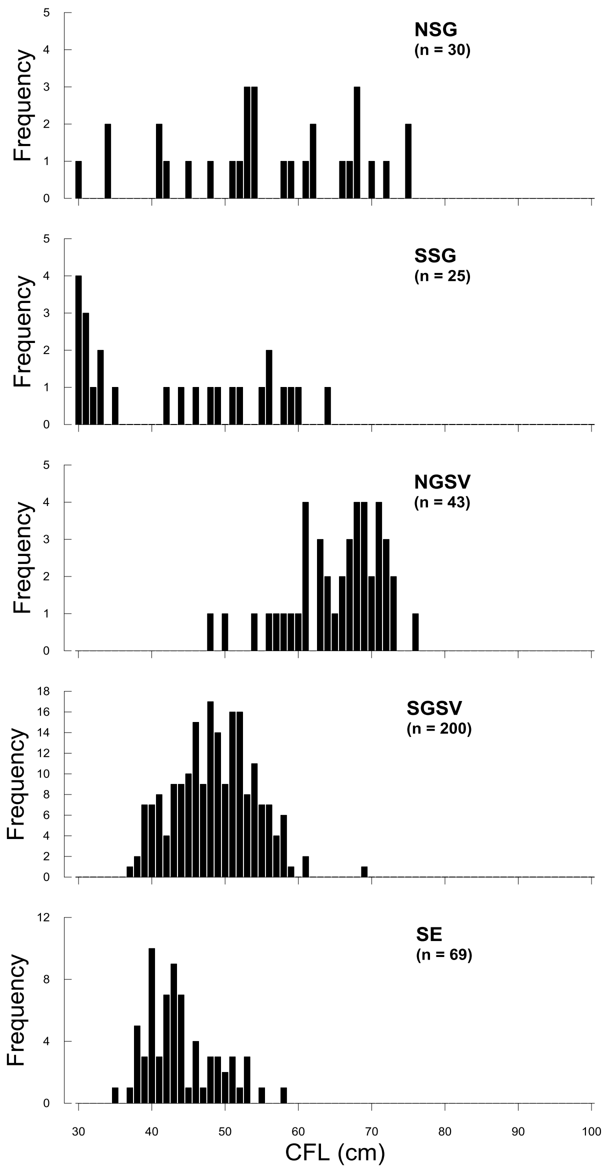

Fig. 3.14 Size frequency distributions of snapper from the 2001 year class that were sampled in 2009 from the five South Australian regions. CFL – caudal fork length, NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Spencer Gulf, SE – South East.

The sizes of the 8+ fish varied amongst regions (Fig. 3.14). The fish sizes from NGSV, SGSV and the SE conformed to relatively tight unimodal distributions, although with considerable differences in modal size. Fish from NGSV were predominantly 'large', with an average size of 65.4 cm CFL, which was 17 cm larger than the predominantly 'medium' fish from SGSV and 21.5

cm larger than the ‘small’ and ‘medium’ fish from the SE. The market-sampled fish from NSG and SSG were fewer than from the other regions and more variable in size. Those from NSG were distributed across the ‘large’, ‘medium’ and ‘small’ size categories. Those from SSG were divisible into ‘small’ and ‘medium’ fish. The average size from SSG was 43.1 cm CFL, which was the smallest for all five regions, and considerably smaller than the average size of 55.6 cm for NSG.

Increment width analysis was done for otoliths from 73 snapper from the 2001 year class. These fish varied in size amongst regions, particularly between NSG and SSG, which resulted in intractably heterogeneous variances. The results from the analysis of variance suggested that fish from NGSV were significantly larger than those from the other regions including SGSV (Fig. 3.15).

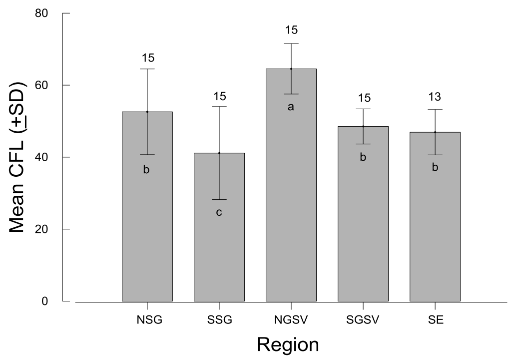

Fig. 3.15 Average size (cm) of snapper from the 2001 year class whose otoliths were compared amongst regions. Sample sizes are indicated above the error bars and results from Student-Newman-Keuls tests are indicated as pronumerals below the error bars. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Regional Comparison of Otolith Characteristics

Major axis measurements

The measurements of otolith size along each major axis and their ratios had homogeneous variances and so were not transformed prior to analysis. Along each axis, the otoliths from NGSV were significantly larger than those from the other four regions (Fig. 3.16). For NSG, the mean sizes of otoliths along Axes II and III were marginally bigger than those for the other regions but the mean size along Axis V was actually smaller, suggesting possible regional variation in the relative growth rates along the different axes that influenced otolith shape. This was confirmed through analyses for the two ratios of the otolith measurements, i.e. Axis II : Axis V and Axis III : Axis V (Fig. 3.16), which reflected the thickness of the otoliths relative to their widths, thereby representing indices of otolith shape. For both ratios, there were significant differences amongst regions. For the ratio of Axis III : Axis V in particular, the otoliths from NSG and SSG had significantly higher values indicating that they were thicker relative to their width than were those from NGSV, SGSV, and SE (Fig. 3.16). This demonstrates regional differences in the relative growth rates of the otoliths in these two dimensions.

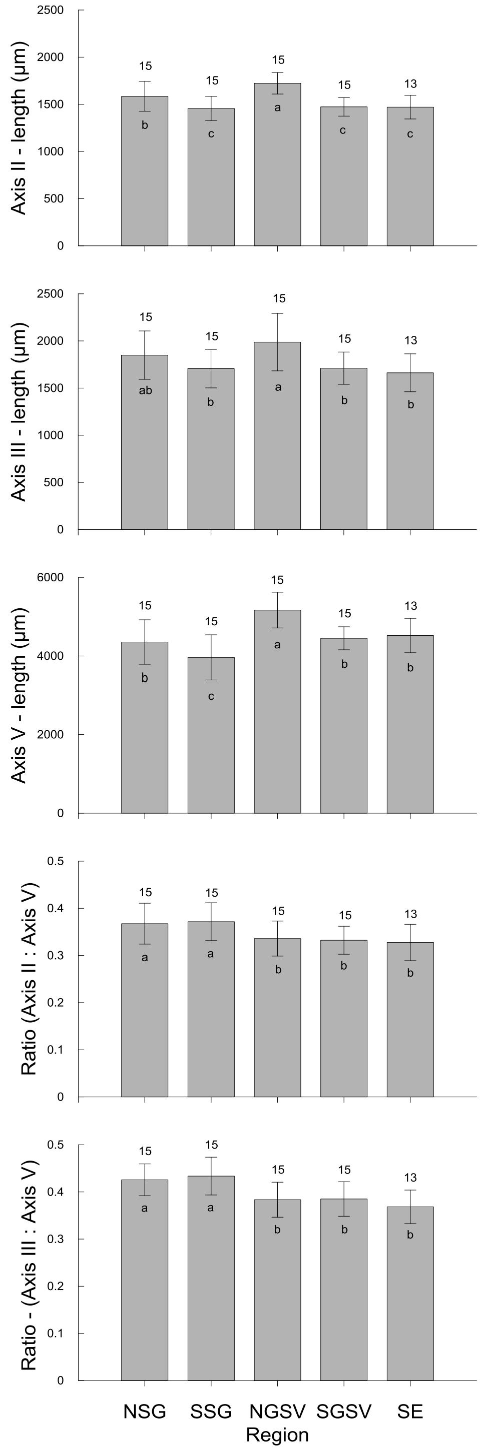

Fig. 3.16 Regional comparisons of mean (+SD) axis measurements and ratios of measurements from TS-sections of otoliths from the 2001 year class for the five South Australian regions. The sample sizes are indicated above error bars whilst results from Student-Newman-Keuls tests are indicated by pronumerals below error bars. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Increment Measurements

The otoliths from the 2001 year class that were sampled in 2009 had eight complete opaque zones. For each region, the increment widths declined exponentially along Axis V, from V-1 to V-8 (Fig. 3.17a). The repeated measures ANOVA indicated significant differences for each of the two main factors of years and regions as well as a significant interaction between them. Comparison of the trajectories of increment widths indicates several patterns of variation (Fig. 3.17). For each of PPB, SE and SGSV, increment V-1 was considerably broader than for NGSV, NSG and SSG. In contrast, V-2 and V-3 for PPB, SE and SGSV were considerably smaller than for the other three regions. From V-4 onwards, there was considerable divergence amongst the regions in these two groups.

For Axis II, the regional differences in the patterns of declining increment widths were largely consistent with those for Axis V (Fig. 3.17b). The most obvious regional differences were the declines between increments II-1 and II-2, particularly for SE, SGSV and PPB. Increment widths for NSG and SSG were similar until II-5, after which they subsequently diverged. Otoliths from NGSV demonstrated the near largest increment widths for II-2 to II-8, which is consistent with them having the broadest axis measurements (Fig. 3.16).

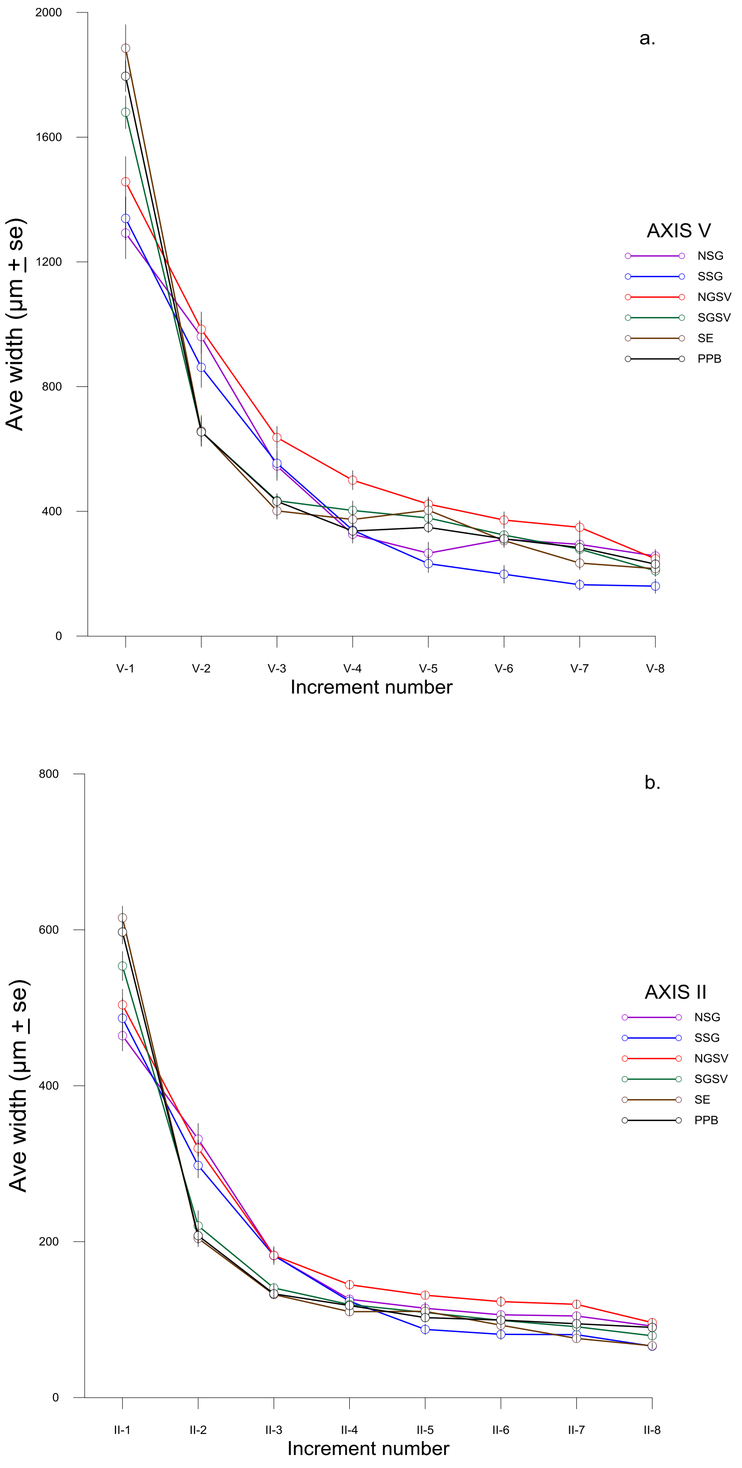

Fig. 3.17 Regional comparison of average increment widths across otoliths from the 2001 year class from the centre to the edge along Axes II and V for otoliths (for location of axes in the otolith TS-section refer Fig. 3.1). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Classification of otolith axes

For Axes II, III and V the chi-squared tests indicated that the grades differed significantly amongst regions (Axis II – $X^2 = 41.9$, df = 12, $p < 0.005$; Axis III – $X^2 = 33.4$, df = 12, $p < 0.005$, Axis IV - $X^2 = 16.0$, df = 12, $0.1<p<0.25^{ns}$; Axis V - $X^2 = 41.6$, df = 12, $p < 0.005$) (Fig. 3.18). For SGSV, SSG, and SE there were more otoliths assigned Grades 1 and 2 whilst NGSV and NSG had more otoliths assigned to Grades 3 and 4, i.e. were clearer and more easily interpreted. Despite a non-significant statistical result for Axis IV, the data generally indicated regional differences in the clarity and interpretability of the otolith structure across the various axes of the TS-sections from the 2001 year class.

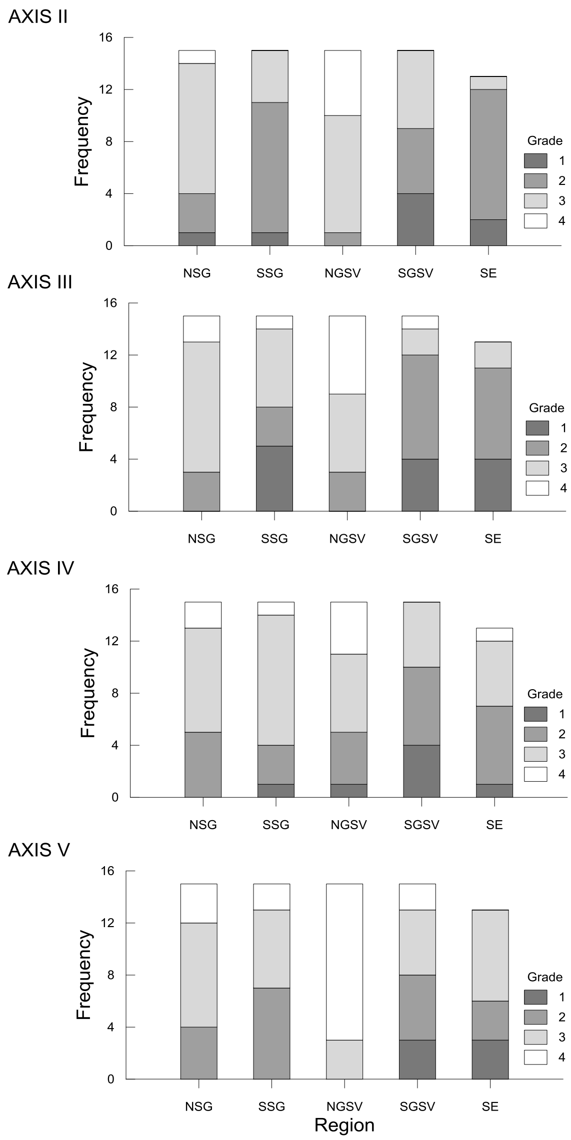

Fig. 3.18 Results from the classification of the four axes (II – V) for otoliths from the 2001 year class sampled from different regions, according to the clarity and interpretability of the otolith structure. Grades: 1 – cannot interpret; 2 – poor; 3 – good; 4 – excellent. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Optical density measurements

The estimates of optical density of the opaque and translucent zones declined towards the otolith edges (Fig. 3.19).

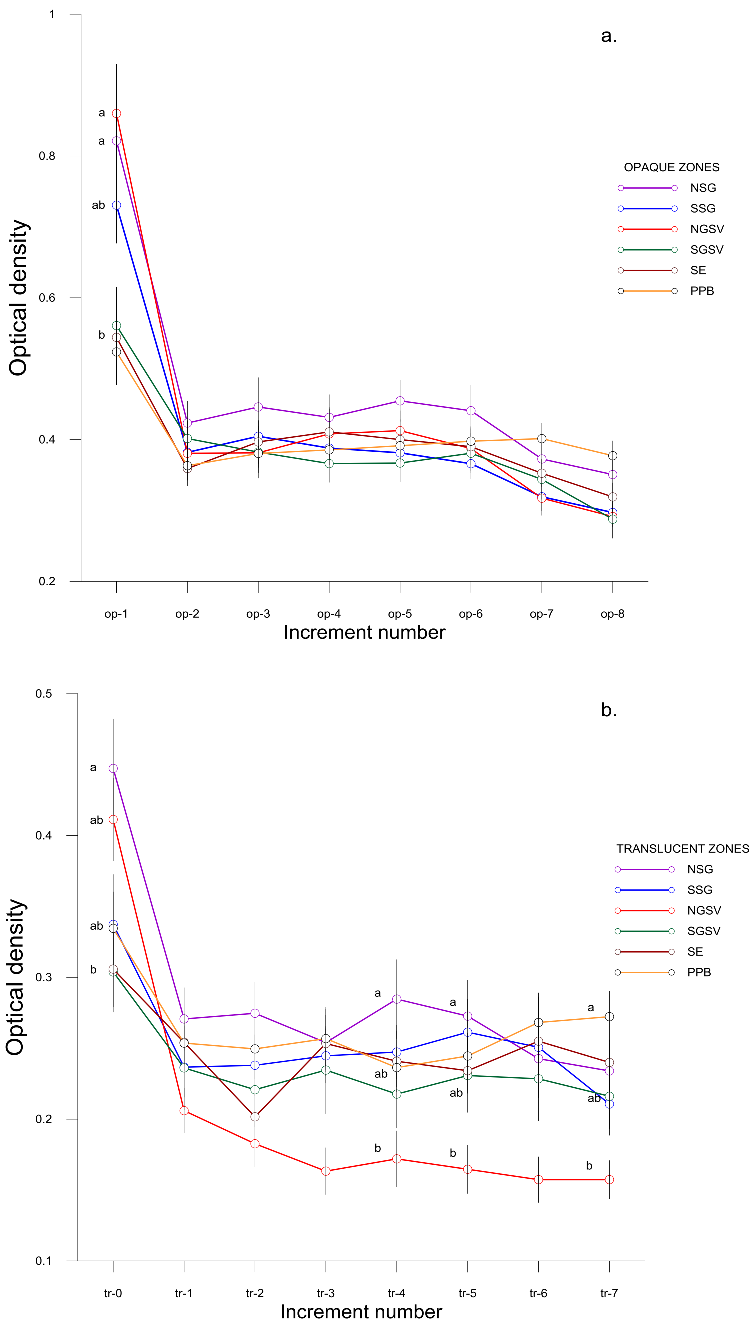

Fig. 3.19 Regional comparison of estimates of optical density measured across Axis V for otoliths from the 2001 year class. a. measurements for the opaque zones. b. measurements for the translucent zones. Results for MANOVAs for each increment are presented in Table 3.2, and results from *a posteriori* comparisons for individual increments are indicated on figure as pronumerals. For increment numbers refer to Fig. 3.1. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

Split-plot repeated measures ANOVAs were done for these trajectories with the measures of optical density in the opaque and translucent zones being the dependent variables. Also, for each increment a MANOVA was done, with the two dependent variables being the respective measures of optical density for the opaque and translucent zones. The former analysis identified a significant interaction between regions and increment number, which indicated that the pattern of variation in optical density across the otoliths varied amongst regions. The results from the MANOVAs identified that the only opaque zone for which optical density differed amongst regions was for op-1 (Table 3.2). For this increment, each of NSG, SSG and NGSV had considerably higher levels of optical density than did SGSV, SE and PPB (Fig. 3.19). Although for each of op-3 to op-6, the otoliths from NSG had consistently higher levels of optical density there were no significant differences amongst regions.

For the translucent zones the repeated measures ANOVAs also indicated an interaction between regions and increment number. The MANOVAs identified significant differences amongst regions for each of tr-0, tr-4, tr-5 and tr-7 (Table 3.2, Fig. 3.19). For the measures for tr-0, the otoliths from NSG and NGSV were again highest, and significantly higher than for SGSV and the SE, with those from SSG and PPB having intermediate levels. For each of tr-4, tr-5 and tr-7, the measures for NGSV were significantly lower than those from several of the other regions.

Table 3.2 Results from MANOVAs for optical density data for the 2001 fish sampled in 2009. For each increment, the data shown include the Wilk's Lambda value from the MANOVA and the probability of a significant difference amongst regions. The table then indicates the results for the two dependent variables for each increment number. Note that a Bonferroni adjusted alpha level of 0.025 was used to assess significance for the two dependent variables.

Increment number	Wilk's Lambda (probability)	Dependent variable	Probability
INC-1	0.643 (0.000*)	op-1	<0.001*
		tr-0	0.006*
INC-2	0.829 (0.090^{ns})	op-2	0.475^{ns}
		tr-1	0.340^{ns}
INC-3	0.792 (0.026*)	op-3	0.590^{ns}
		tr-2	0.045^{ns}
INC-4	0.707 (0.001*)	op-4	0.657^{ns}
		tr-3	0.037^{ns}
INC-5	0.735 (0.003*)	op-5	0.247^{ns}
		tr-4	0.011*
INC-6	0.752 (0.006*)	op-6	0.524^{ns}
		tr-5	0.010*
INC-7	0.775 (0.014*)	op-7	0.064^{ns}
		tr-6	0.030^{ns}
INC-8	0.701 (0.001*)	op-8	0.034^{ns}
		Tr-7	0.001*

3.3.4 2004 Year Class

Regional Comparison of Fish Sizes

There were considerable differences amongst regions in the numbers of 5+ fish from the 2004 year class that were processed in market sampling in 2009 that ranged from 83 fish for SGSV down to only 13 fish from the SE (Table 3.1). The size distributions differed amongst regions (Fig. 3.20). Those for NSG, SSG and NGSV involved the ‘small’ and ‘medium’ size classes and broadly overlapped between regions. In contrast, the sizes of fish from SGSV and SE conformed to tight unimodal distributions. The fish from NGSV had a mean size of 46.5 cm CFL, which was 5.6 cm larger than those from SGSV and 11.4 cm larger than those from the SE. The fish from NSG and SSG involved the broadest size ranges, whilst some fish from SSG were the smallest from any region.

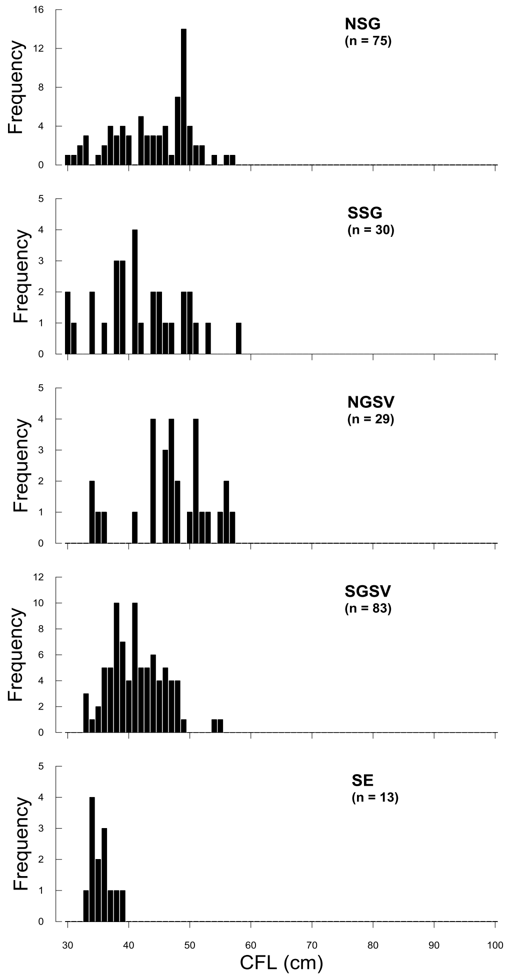

Fig. 3.20 Size frequency distributions of snapper from the 2004 year class that were sampled in 2009 from the five South Australian regions. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Otoliths from 128 snapper were considered in the increment width analyses. Because of the broad size ranges from NGSV, NSG and SSG compared to SGSV and the SE, the data had intractably heterogeneous variances. The results of the analysis of variance that compared the sizes of fish amongst regions suggested that the fish from NGSV were significantly larger than those from SSG and SGSV, which were larger than those from the SE (Fig. 3.21).

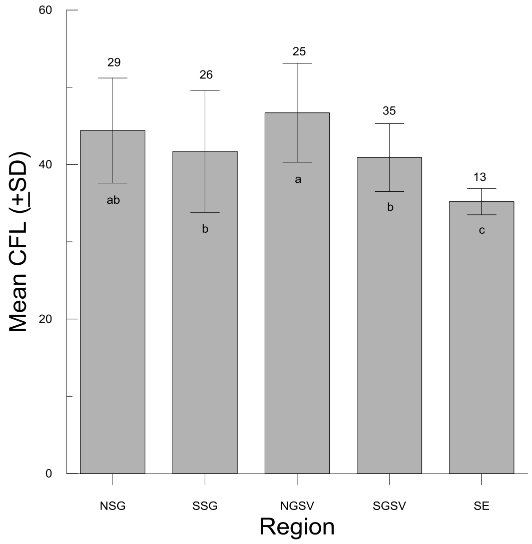

Fig. 3.21 Average size (cm) of snapper from the 2004 year class whose otoliths were compared amongst regions. Sample sizes are indicated above the error bars and results from Student-Newman-Keuls tests are indicated as pronumerals below the error bars. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Regional Comparison of Otolith Characteristics

Major axis measurements

For each of the major axes as well as the ratios of Axis II : Axis V and Axis III : Axis V, the data had homogeneous variances, and so were not transformed prior to analysis. These analyses indicated significant regional differences in axis length for each of Axes II, III and V (Fig. 3.22). The otoliths from NGSV usually had the largest mean size, significantly larger than those from SSG and the SE. Those from NSG and SGSV were generally intermediate in size and did not differ from the other regions. There were no significant differences amongst regions for the estimates of ratios of Axis II : Axis V and Axis III : Axis V (Fig. 3.22).

Increment measurements

Otoliths from the 2004 year class that were sampled in 2009 had five complete opaque zones. There were also some similar-aged fish from PPB, whose otoliths were directly comparable to those from the South Australian regions. For the otoliths from the six regions, the average increment widths declined exponentially between the centres and edges along both Axis V and Axis II (Fig. 3.23). The increment width data along Axis V had heterogeneous variances and so were transformed using log(x + 1), prior to analysis. The repeated measures ANOVA on transformed data indicated significant differences for each main factor of increment number and regions as well as a significant interaction between them. Comparison of the trajectories of increment widths indicates several patterns of variation. For both PPB and the SE, V-1 was broad, but then declined rapidly to relatively low values for V-2 and V-3. Subsequently, the V-4 and V-5 values for these two regions remained low and then diverged. Whilst the V-1 values for

NGSV and SGSV were also relatively high, their V-2 and V-3 values were also relatively high and similar before eventually diverging for increments V-4 and V-5. NSG and SSG had similar low values for V-1. Their values for V-2, V-3 and V-4 subsequently remained at similar levels.

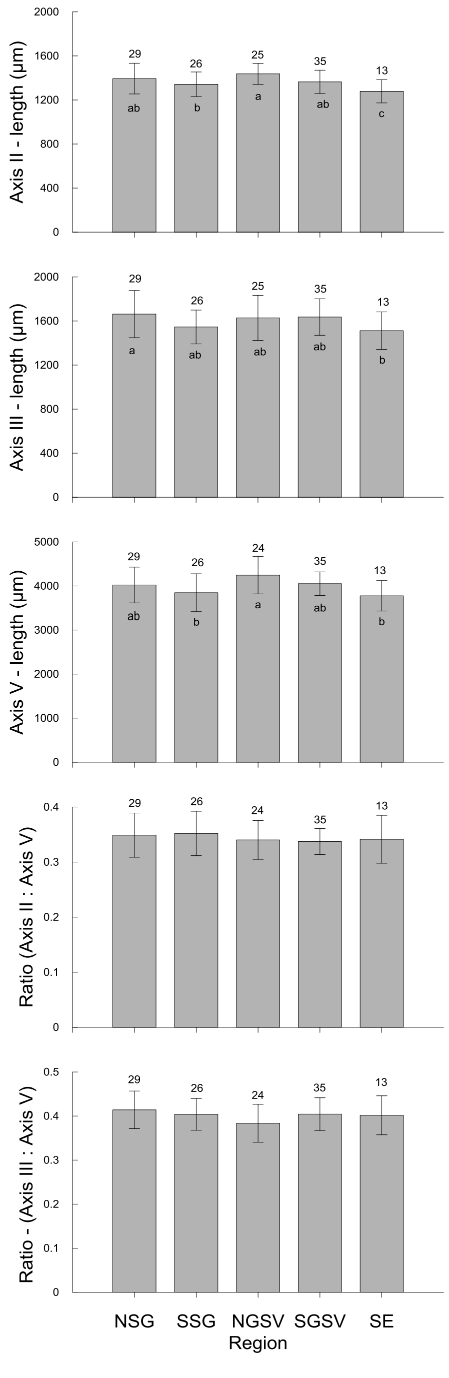

Fig. 3.22 Regional comparisons of mean (+SD) axis measurements and ratios of measurements from TS-sections of otoliths from the 2004 year class for the five South Australian regions. The sample sizes are indicated above error bars and results from Student-Newman-Keuls tests are indicated by pronumerals below error bars. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

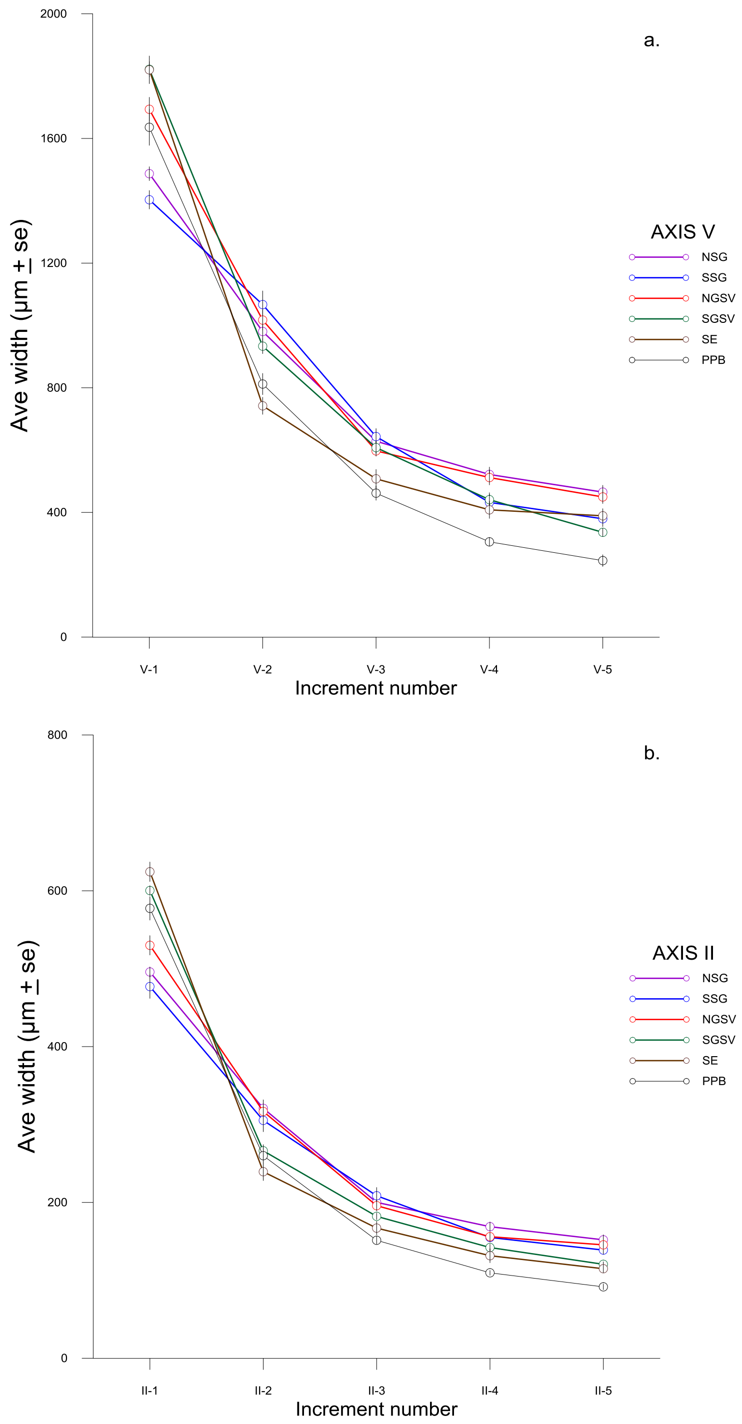

Fig. 3.23 Regional comparison of increment widths across otoliths from the 2004 year class from the centre to the edge along Axes V and II (for location of axes in the TS-section refer to Fig. 3.1). Conventions as for Fig. 3.14. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

The data for Axis II also had heterogeneous variances and so were transformed prior to analysis. The repeated measures analysis again identified a significant interaction, which indicated regional variation in the patterns of increment width across the otoliths. The three regions of SGSV, SE and PPB each had broad II-1 increments. For the subsequent increments of II-2, II-3, II-4 and II-5, increment width was higher for NGSV, NSG and SSG than for the three southern regions (Fig. 3.23).

Classification of otolith axes

For Axes II and V, the proportions of otoliths assigned to particular grades were compared using a chi-squared contingency table. For Axis II, the grades differed significantly amongst regions (χ^2 = 44.4, df = 12, $p < 0.005$) (Fig. 3.24). Most otoliths from NSG, NGSV and SGSV were assigned to Grades 3 or 4. In contrast, those from SSG and SE had fewer Grade 3 otoliths, and more assigned to Grade 2. The results for Axis V demonstrated comparable regional differences (χ^2 = 43.9, df = 12, $p < 0.005$), although with marginally more otoliths assigned to Grades 3 and 4. Overall, there were regional differences in clarity of otolith structure across the two axes of the TS-sections.

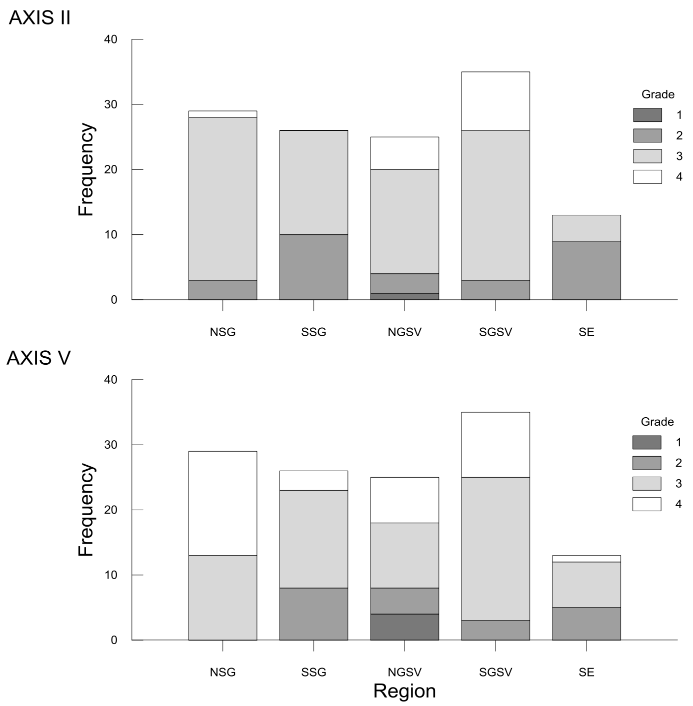

Fig. 3.24 Results from the classification of Axes II and V for otoliths from the 2004 year class from different regions according to the clarity and interpretability of the otolith structure. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East.

Optical density measurements

The estimates of optical density were lower for the middle and peripheral increments than for op-1 and tr-0 (Figs. 3.25a, b). For the data for both the opaque and translucent zones there were several violations of the assumptions of the multivariate tests. Consequently, prior to analysis the estimates of optical density for the opaque and translucent zones were transformed using log(x + 0.01). Subsequently, the data had homogeneous variances but the heterogeneous covariance matrices remained, thus requiring a cautious approach to further data interpretation. For both the opaque and translucent zones the repeated measures analyses of variance identified significant interactions between the main factors of increment number and regions, which meant in each case the pattern of variation in optical density across otoliths varied amongst regions. The MANOVAs subsequently identified that these interactions were driven by regional differences only for INC-1 and INC-5, which in particular, related to differences at tr-0 and op-5 (Table 3.3). For tr-0, the regions of NSG, SSG and PPB had higher values than did SGSV, whilst NGSV and SE had intermediate values (Fig. 3.25). For op-5, PPB had the highest values that were significantly greater than for NSG, SGSV, SE and SSG.

Table 3.3 Results from MANOVAs for optical density data for the 2004 fish sampled in 2009. For each increment, the data shown include the Wilk's Lambda value from the MANOVA and the probability of a significant difference amongst regions. The table then indicates the results for the two dependent variables for each increment number. Note that a Bonferroni adjusted alpha level of 0.025 was used to assess significance for the two dependent variables.

Increment number	Wilk's Lambda (probability)	Dependent variable	Probability
INC-1	0.763 (<0.001*)	op-1	0.065^{ns}
		tr-0	<0.001*
INC-2	0.859 (0.021*)	op-2	0.072^{ns}
		tr-1	0.182^{ns}
INC-3	0.856 (0.017*)	op-3	0.937^{ns}
		tr-2	0.035^{ns}
INC-4	0.870 (0.037^{ns})	op-4	0.220^{ns}
		tr-3	0.238^{ns}
INC-5	0.774 (<0.001*)	op-5	0.008*
		tr-4	0.136^{ns}

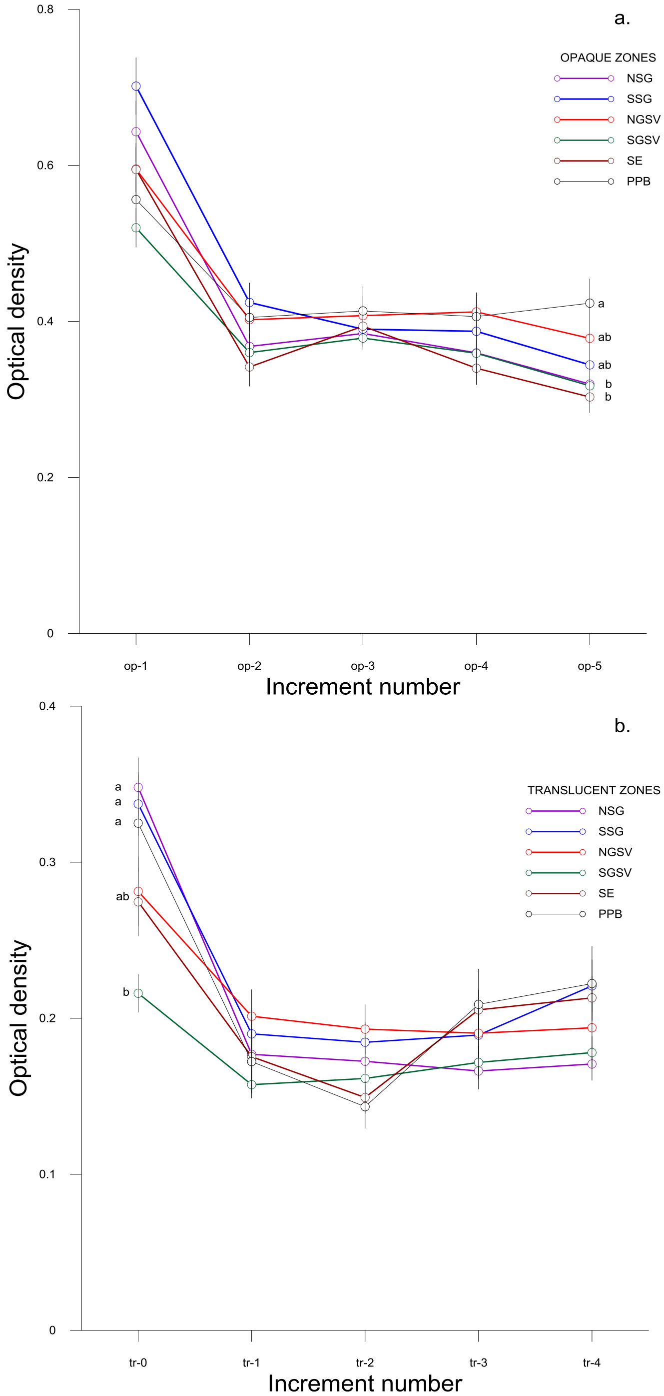

Fig. 3.25 Regional comparison of estimates of optical density measured across Axis V for otoliths from the 2004 year class. a. measurements for the opaque zones. b. measurements for the translucent zones. Results for MANOVAs for each increment are presented in Table 3.3, and results from *a posteriori* comparisons for individual increments are indicated on figure as pronumerals. For increment numbers refer to Fig. 3.1. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

3.4 Discussion

3.4.1 Regional and year class comparisons

Determining stock structure for a fishery species can be difficult. This is often based on comparing phenotypic characteristics amongst regional populations and interpreting differences in terms of the periods of occupancy of different environments, from which inferences about stock structure can be drawn. Furthermore, the chronological macrostructure of otoliths provides refined, age-related information that can provide insight into population processes that is relevant to stock structure (Kerr and Campana 2014). Such chronological structure can point to whether fish captured from different regions may have originated from the same or different nursery areas, and when any large-scale inter-regional movement may have occurred. This chapter addressed such questions for South Australian snapper based on physical characteristics of otoliths and the fish from which they came.

1991 Year Class

There were not dramatic differences in the characteristics of fish from the different regions. Fish and otolith sizes were largely consistent amongst the four South Australian gulf regions. Regardless of where captured in 2003, these 12+ fish were generally ‘large’ with the exception of a considerable number of ‘small’ and ‘medium’ fish captured from SSG. Such small fish influenced the mean size of otoliths from this region, which were marginally smaller along Axis II than for the other regions.

The classification of the otolith axes in terms of clarity and interpretability also showed marginal regional differentiation. The otoliths from the two southern regions tended to be less clear than those from the northern regions. Whilst these data are consistent with some regional separation, the considerable within-region variation in these grades meant that there could have been some mixing of fish between the northern and southern regions.

The increment width data along Axes V and II provided useful age-related data for comparison amongst regions. These data showed little regional differentiation for increments INC-1 to INC-3, i.e. the first formed increments during years 1 to 3 of the fishs’ lives. This is consistent with the hypothesis that all fish originated from only one or two nursery areas, which are likely to be located in the northern gulfs (Fowler and Jennings 2003, Fowler et al. 2005). However, the regional separation for INC-4 to INC-9 suggests that some fish may have undertaken some inter-regional movement through the age range of 4 to 9 years and taken up residence in the southern regions. From these data it is not possible to determine the relative contributions of NSG and NGSV to the southern regions. However, given the dominance in spawning biomass from NSG that is evident in the fishery statistics, it is expected that a significant contribution would have come from this region (Fowler et al. 2013). The otoliths from PPB had sufficiently different increment widths to indicate that it was highly unlikely that fish from the 1991 year class in the South Australian regions originated from PPB.

1997 Year Class

The results from the inter-regional comparison of otoliths for the 1997 year class from the four gulf regions of South Australia in 2008 were similar to those for the 1991 year class. The catches of these 11+ fish from the 1997 year class from NSG and NGSV were dominated by 'large' fish. The size distribution for SSG again included 'stunted fish', whilst the few fish captured in SGSV also covered a broad size range. The regional comparison of otolith sizes reflected the influence of small fish in these two southern regions. The results of the classification of otolith clarity showed no significant regional differentiation. So, apart from the likely presence of some slow-growing residents in SSG and SGSV, these data showed little evidence for regional differentiation.

The increment width analysis also showed no significant regional differentiation until the fourth increment. These data are consistent with fish sampled from the different regions having originated from one or two nursery areas followed by the dispersion of fish to the southern regions from the ages of four to seven years. Whilst the otoliths from PPB had the broadest first increment (V-1, II-1), the difference from the South Australian otoliths was less than for 1991 fish, which meant that it was not possible to exclude the unlikely hypothesis that the South Australian fish had originated in and subsequently emigrated from PPB.

2001 Year Class

Whilst the data from the 1991 and 1997 year classes showed relatively subtle regional differences, the data for the 2001 year class demonstrated significant differences amongst several groups of regions. Fish from the northern gulfs were relatively large compared to 'medium' fish from SGSV and SE, which also influenced otolith size. Increment width analysis indicated that the otoliths from PPB, SE and SGSV were very similar for INC-1, INC-2 and INC-3 after which they diverged. These otoliths clearly had different increment widths from the first increment onwards from those from NSG, SSG and NGSV. This suggests that, based on the first three increments, the otoliths fell into two regional groupings. The optical density data were also largely consistent with this spatial differentiation. At op-1, i.e. the optical density at the first annual opaque zone, the otoliths from NSG, NGSV and SSG had considerably higher values than those from the three southern regions of PPB, SE and SGSV. The measures of optical density at tr-0 showed similar but marginally less clear regional differentiation.

The similarity in trajectories of increment widths and optical density for the first few increments in the otoliths from PPB, SE and SGSV supports the hypothesis that these fish had a shared origin that differed from that of the fish from NSG, SSG and NGSV. The likely origin for the former group is PPB, which is the primary nursery area for the Western Stock of Victoria (Hamer et al. 2005, 2006, 2011). The fish are likely to have spent the first couple of years in this nursery area, after which some left and eventually moved hundreds of kilometres westwards. It appears that whilst many reached the SE region, others moved even further to SGSV.

The comparison of otoliths between NSG and SSG also showed similarities. These trajectories of increment widths were similar between INC-1 to INC-5, after which they diverged for the last three increments. These results suggest a shared origin, most likely in the nursery area in NSG, where fish remained for the first few years before some moved to SSG. The otoliths from NGSV were similar to those from NSG and SSG. From these data it is not possible to empirically differentiate between the alternative hypotheses that these fish originated in NGSV or in NSG and subsequently moved to NGSV.

The most surprising result from the regional comparisons for the 2001 year class is the difference between the otoliths from NGSV and SGSV. The comparative data for these two regions are more consistent with the fish from SGSV having originated in PPB and migrating 800 km westward, compared with having originated in NGSV and moving only 150 km southwards.

2004 Year Class

Fish from the 2004 year class that were collected in 2009 were in the 5+ age class. This was the youngest year class considered in this study, which meant that there had been less time for regional differences to have become established compared to the other year classes. Nevertheless, there were differences amongst regions in the sizes of fish and their otoliths. Fish from the SE were the smallest considered, whilst those from SGSV and SSG were smaller than those from the northern gulfs. The classification of otoliths also differed amongst regions. Overall, such data demonstrated differentiation consistent with fish from different regions having occupied different marine environments for considerable parts of their lives.

The increment width analysis also demonstrated regional differences, although the interpretation was more ambiguous than for the 2001 year class. Fish from the SE and PPB had similar trajectories of increment widths along both Axes V and II. However, the results for fish from SGSV were less clear. For Axis V the trajectories were more similar to those from NGSV, whereas along Axis II they were more similar to those from PPB and the SE. Furthermore, the optical density data for tr-0 from SGSV differed from those of PPB and SE. Despite the ambiguity with respect to the origins of fish from SGSV, the remaining data suggest that the fish from the SE originated in PPB and moved sometime from their third year onwards. The otoliths from NSG and SSG were also quite similar suggesting that fish from the latter region had originated in NSG and subsequently moved southwards. The increment widths at V-1 and II-1 for fish from NGSV differed somewhat from those of NSG, providing some empirical evidence for different origins.

3.4.2 Conclusions

As part of the 'multiple-technique' approach for assessing large-scale movement and stock structure for snapper amongst regional populations of SA, the physical characteristics of otoliths from four strong year classes were compared amongst regions. The otoliths for each year class showed some regional differences that reflected spatial differentiation that was consistent with the regional populations not consisting of a single, large, inter-mixed stock. Rather regional differences in otoliths sizes, increment clarity, increment widths and optical density were consistent with individual fish spending considerable parts of their lives associated with particular regions. The analysis of the age-related data from the chronological structure of otoliths provided empirical evidence that fish from the northern and southern regions of the gulfs had shared origins and that separation occurred through emigration that occurred from approximately three years of age. For the 1991 and 1997 year classes, there was no evidence of fish from PPB in the South Australian gulf waters. For the 2001 year class, increment width data suggested that fish from the SE and SGSV had originated in PPB. For the 2004 year class, the data suggested that the fish from the SE had come from PPB, whilst those from SGSV had originated in the northern gulfs. These hypotheses were tested using otolith chemistry analyses in Chapter 4.

4. Otolith chemistry

Anthony Fowler, Paul Hamer, Jodie Kemp

4.1 Introduction

One of the most significant analytical approaches for investigating stock structure for fishes that has developed over the past 20 years is the analysis of otolith chemistry (Campana 1999, Elsdon et al 2008, Sturrock et al. 2012). The basis of this methodology is that as a fish's otoliths (or earbones) grow they incorporate some chemical elements as impurities in minor and trace quantities from the aquatic environment at rates that are influenced by the physico-chemical environment that the fish is exposed to at that time (Campana 1999). The consequence of this is that the otoliths of every fish ultimately manifest an 'elemental fingerprint' that reflects the aquatic environments that it has experienced throughout its life (Campana 1999, Campana and Thorrold 2001, Sturrock et al. 2012). Such 'elemental fingerprints' then act as natural tags that can be used to differentiate between fish that have lived, at least part of their lives, in different places that have different environmental characteristics (Campana 1999). The interaction between physical environmental characteristics and the physiological processes that culminate in the chemical signal in otoliths are complex and differ between elements, and are not yet fully understood (Sturrock et al. 2012, 2014). However, this does not preclude using otolith chemistry data to address issues of connectivity through large-scale movement between regions and populations, which contribute to understanding stock structure of fish (Gillanders 2002, Fowler et al. 2005, Hamer et al. 2006, Elsdon et al. 2008, Steer et al. 2009, 2010, Fairclough et al. 2013, Kerr and Campana 2014, Gillanders et al. 2015, Hughes et al. 2015).

The usefulness of otolith chemistry for determining stock structure is based on several unique characteristics of otoliths and how they grow (Campana and Thorrold 2001, Sturrock et al. 2012). This occurs through the daily deposition of calcium carbonate crystals onto a fibroprotein organic matrix (Campana and Neilson 1985) through a process of biomineralisation from the endolymph fluid, where there is no epithelial contact (Campana 1999, Campana and Thorrold 2001). This process of incremental growth continues throughout the life of the fish, even when somatic growth rate declines for adult fish (Campana and Thorrold 2001, Fowler 2009), producing a sequentially-formed, acellular, crystalline structure. Furthermore, the otolith is metabolically inert, i.e. it is never subsequently reworked through resorption and re-deposition as occurs with skeletal bone (Campana 1999, Sturrock et al. 2012). This results in the otolith being a layered structure from its core to edge that reflects the entire chronology of the fish's life from its early life history through to the juvenile and adult life history stages. The 'elemental fingerprint' across the otolith's chronological structure relates to the history of aquatic environments that the fish has experienced throughout its life. By retrospectively accessing and interpreting this information can inform about the place-of-origin of the fish and any large-scale movement that occurred throughout its life

(Fowler et al. 2005). Comparison of such data within and amongst populations can be used to address issues of stock structure (Fowler et al. 2005, Hamer et al. 2006, Steer et al. 2009).

Snapper (*Chrysophrys auratus*) is the most significant coastal finfish species of southeast Australia, with adjacent regional fisheries along its continuous coastal distribution from South Australia (SA) to central Victoria (Fig. 4.1). Over the past decade, these numerous regional fisheries have experienced major changes in fishery production (Fowler et al. 2013). Through this period, SA made the highest State-based contribution to the national commercial catch of snapper, which corresponded to a significant change in the spatial structure of the productivity of SA's regional fisheries. Historically, SA's fishery was dominated by Spencer Gulf, particularly the relatively small region of Northern Spencer Gulf (Fowler and McGlennon 2011, Fowler et al. 2013). However, since 2007, the annual catches from this region have decreased significantly and by 2014 had fallen to a historically low level (Fowler and McGarvey 2014). Over the same period, the catches increased dramatically in other regions, particularly Northern Gulf St. Vincent (NGSV) and the south eastern coastal region of the State (SE). The demographic processes responsible for these contrasting changes in the different regions and the extent to which they are related amongst regions are not understood. The unprecedented regional increases in fishable biomass and productivity in NGSV and the SE may relate to: local demographic processes of reproduction and recruitment of the 0+ age class; or inter-regional immigration of very large numbers of juvenile or adult fish from other regions. Differentiating between these different demographic processes that operate at different spatial scales has implications for the stock structure and therefore for determining the appropriate spatial scale and mechanisms for managing these various regional fisheries.

The study described in this chapter aimed to resolve the demographic processes responsible for the significant changes in SA's snapper fishery over the past decade, based on the chronologies of elemental fingerprints in the transverse sections of their otoliths. Several previous otolith chemistry studies have been done for the snapper populations of south eastern Australia. One study done in SA compared the elemental profiles of otoliths from a single year class amongst several adjacent regions and determined that there are primary nursery areas located in the northern parts of both Spencer Gulf and Gulf St. Vincent (Fowler et al. 2004, 2005). These regions support source populations from which snapper later disperse to the southern gulfs and the continental shelf. Similarly, Port Phillip Bay (PPB) in Victoria has been identified as the primary source for the Western Victorian stock that extends hundreds of km westward from the bay (Hamer et al. 2005, 2006, 2011). Otolith chemistry studies done in Western Australia have identified likely differences in life history characteristics, movement patterns and the scale of stock structure between Shark Bay and the southern coastal populations (Edmonds et al. 1989, Bastow et al. 2002, Fairclough et al. 2013).

The overall aim of this study was to develop an understanding of the demographic processes that led to the regional changes in fishery productivity in the South Australian snapper fishery over the past decade. The approach used was to increase the spatial and temporal scales of the earlier otolith chemistry studies that were described above. Here, adult otoliths were considered from six regions from across SA and Victoria and from four different year classes, i.e. 1991, 1997, 2001 and 2004. These year classes represent different stages in the recent history of the snapper fisheries in the two jurisdictions. For each year class, the chemistry across the chronological structure of the otoliths was compared amongst regions to address hypotheses about the nursery areas from which the fish originated and to determine when during their lives that any inter-regional movement occurred that led to the replenishment of regional populations. In this context, the otolith chemistry analyses were used to address several specific questions. First, were the respective increase and decrease in biomass in NGSV and NSG independent ecological phenomena or did large numbers of fish move from the latter region to the former? Where did the fish that were responsible for the recent increase in biomass in the SE region originate? Which nursery area(s) contributed to the replenishment of populations in Southern Spencer Gulf (SSG) and Southern Gulf St. Vincent (SGSV)?

4.2 Methods

4.2.1 Sample collection

This study compared the elemental fingerprints across the chronological structure of the transverse (TS) sections of otoliths from six geographic regions of south eastern Australia. These were the five SA regions of NSG, SSG, NGSV, SGSV, and the SE, as well as PPB in Victoria (Fig. 4.1). The inter-regional comparisons involved fish from four different year classes (birth years), i.e. 1991, 1997, 2001 and 2004 (Table 4.1), which were strong year classes in some of the six regions (Chapter 2 this report; Hamer and Jenkins 2004, Fowler and McGlennon 2011, Fowler et al. 2013). As far as possible, the otoliths from each year class were collected in the same year. This meant that the regional comparisons involved fish that were the same age and had lived through the same period of time, thereby minimising the possibility of confounding the spatial comparisons of otolith chemistry with temporal environmental variability. The only exceptions to this were for the 1991 and 1997 year classes from PPB that were sampled a few years before those from SA (Table 4.1). Otoliths from SA for the 1991 year class were sampled in 2003 and so were 12+ years of age, whilst those from PPB were sampled in 2000 and were 9+ years of age. The 1997 year class was sampled in SA in 2008, whilst the fish from PPB were sampled in 2004. As such, the otoliths from these two year classes for the PPB fish overlapped with those from SA for the first nine and seven years of life, respectively. Otoliths from the 2001 and 2004 year classes from all regions were collected in 2009 (Table 4.1). Note that otoliths were not available from the SE for the 1991 and 1997 year classes due to low commercial catches.
The otoliths from SA were available in an otolith repository that has been developed from a long-term market sampling program (Fowler et al. 2013), primarily undertaken at SA's main commercial wholesale fish market since 2000. For this sampling, researchers visited the fish

market once per week and intercepted commercial catches from the different regional areas of the State. During each visit, snapper from catches were measured and the otoliths from a sub-set of fish were collected. The otoliths from Victoria were sourced from the archives of Fisheries Victoria that have been collected since the early 1990's.

Otoliths were generally removed from each fish within 24 hours of its capture, cleaned and stored in plastic bags until processing. For each year class and region, up to 18 fish were randomly selected from those available in the multi-year otolith collection, depending on the number available (Table 4.1). There were considerable differences amongst regions in the means and ranges of fish size from which the otoliths were used, which is likely to have influenced otolith size (Chapters 2 and 3).

Table 4.1 Details of samples of otoliths considered in the regional otolith chemistry study. For each year class the data show the region and year sampled, the fish age, the number of otoliths considered, as well as the mean (±SD) and range of fish sizes. Regions as for Fig. 4.1. CFL – caudal fork length, SD – standard deviation, NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

Year class	Region	Year sampled	Fish age (years)	n	Mean CFL (±SD) (cm)	Range (CFL) (cm)
1991	NSG	2003	12	16	77.1 (4.8)	69 – 85
	SSG			15	60.4 (11.9)	42 – 79
	NGSV			15	74.7 (5.2)	63 – 85
	SGSV			15	72.9 (3.5)	65 – 78
	PPB	2000	9	18	60.7 (3.4)	55 – 67
1997	NSG	2008	11	18	72.9 (5.8)	62 – 81
	SSG			15	53.3 (16.2)	34 – 78
	NGSV			15	76.5 (5.2)	65 – 84
	SGSV			12	57.9 (12.0)	36 – 76
	PPB	2004	7	18	48.7 (4.4)	40 – 55
2001	NSG	2009	8	15	55.6 (13.7)	30 – 75
	SSG			15	43.3 (13.5)	25 – 64
	NGSV			15	64.4 (7.2)	50 – 76
	SGSV			15	48.1 (4.6)	39 – 56
	SE			13	44.8 (5.7)	38 – 55
	PPB			18	43.5 (5.6)	35 – 55
2004	NSG	2009	5	14	44.0 (8.6)	25 – 56
	SSG			15	42.7 (7.1)	31 – 58
	NGSV			16	47.4 (5.5)	35 – 56
	SGSV			15	40.8 (3.8)	33 – 48
	SE			13	35.1 (1.6)	33 – 39
	PPB			18	30.3 (3.9)	24 – 39

4.2.2 Otolith preparation

A sagitta from each fish was embedded in epoxy resin (Struers Epofix), sectioned to approximately 400 µm in the TS-plane to incorporate the core, and polished with grades of aluminium oxide lapping film lubricated with Milli-Q water. Each polished section was sonicated in Milli-Q water for 5 minutes, liberally rinsed prior to drying in a laminar flow cabinet and stored in a plastic container. The birth year (i.e. year class) was determined from the count of annual increments, the date of capture, and interpretation of the marginal increment, with the birth date of January 1st.

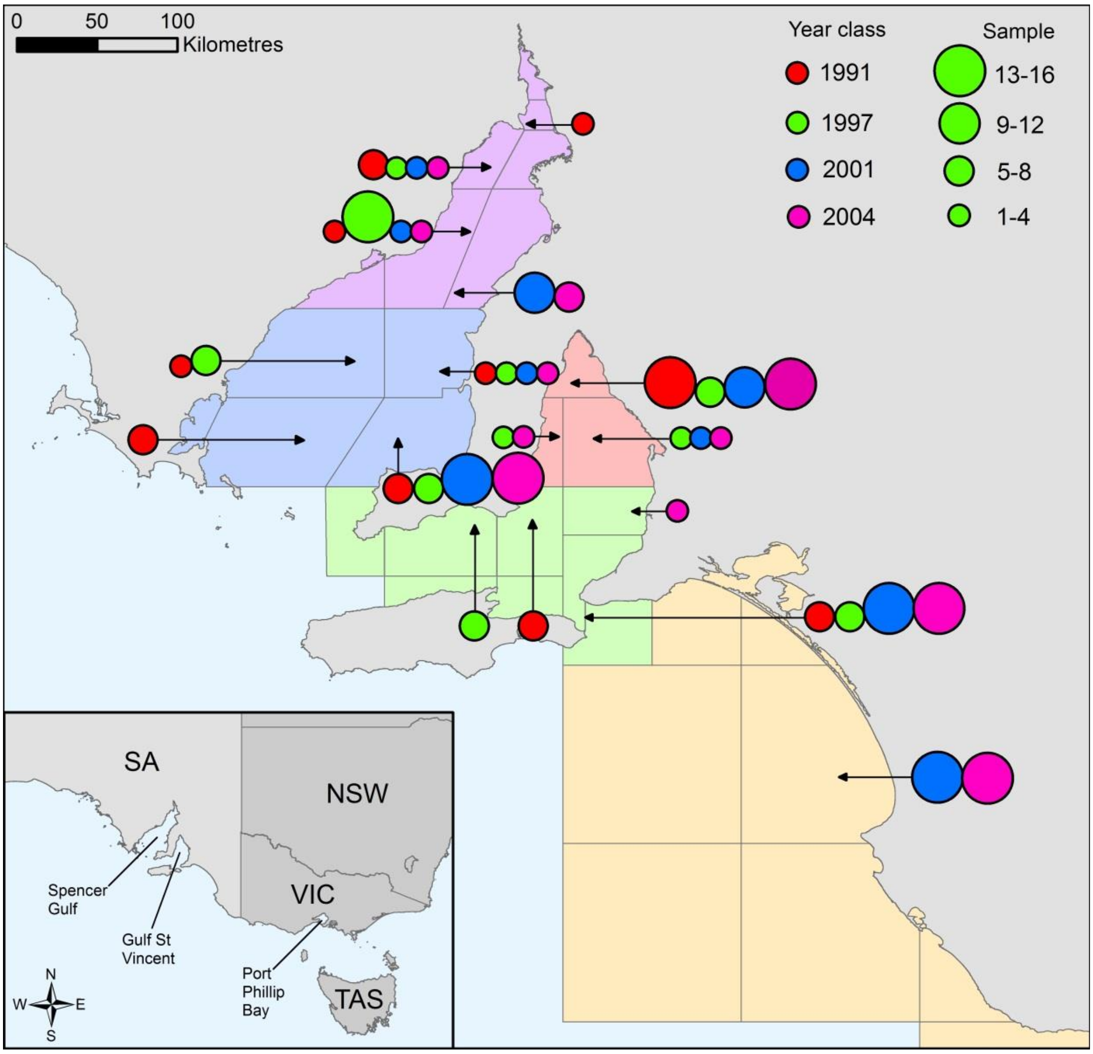

Fig. 4.1 Map of South Australia showing the regions from which snapper otoliths were collected (Northern Spencer Gulf (mauve); Southern Spencer Gulf (blue); Northern Gulf St. Vincent (red); Southern Gulf St. Vincent (green); South East (orange). The lines show the boundaries of the Marine Fishing Areas used for collection of fishery statistics. Coloured symbols represent numbers of otoliths from each year class and each region used in the otolith chemistry analyses. Approximate locations from where the otoliths were collected within each region are indicated by the arrow heads. Inset is a map of south eastern Australia showing the locations of the three primary nursery areas in Northern Spencer Gulf, Northern Gulf St. Vincent and Port Phillip Bay, Victoria.

4.2.3 Elemental analysis

Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS, Laser - New Wave UP213, ICP-MS – Thermo Scientific Element 2, Fisheries Victoria, Queenscliff, Victoria, Australia) was used to obtain age-related element:Ca profiles. The laser was programmed to traverse the otolith section from the core to the margin along the dorsal axis (Axis V) (Fig. 4.2). This axis was chosen for analysis because: it is one of the clearest for differentiating the opaque zones for fish ageing and increment measurement and; being a long axis, it maximised the otolith material available for chemical analysis in each annual increment. Laser settings were: beam diameter 40 µm, fluence 10 J cm^{-2}, and repetition rate 5 Hz, with 10 µm s^{-1} stage movement along the transect path. Ablation occurred in helium that was mixed with argon for injection to the plasma. Each transect path was pre-ablated as a final surface cleaning step with a beam diameter of 100 µm, fluence 6 J cm^{-2}, repetition rate 5 Hz, and 70 µm s^{-1} stage movement along the transect path. The ICP-MS measured the isotopes of Mg^{25}, Mn^{55}, ^{88}Sr, ^{138}Ba, and ^{43}Ca. The latter was used as the internal standard to adjust for variation in ablation yield. The Ca concentration of otolith matrix was 38.8% by weight (Yoshinaga et al. 2000). Blanks were obtained by analysing sample gases for approximately 50 x ICP-MS scans of the selected isotopes prior to sample ablation, and the averages of the blank counts were subtracted from the sample counts prior to calibration. Calibration was achieved with the National Institute of Standards (NIST) 612 certified reference pellet (Lahaye *et al*. 1997). Data are presented as molar ratios to Ca.

Precision and accuracy were assessed by analysing the NIST 612 as an unknown sample with the actual concentrations as reported in Pearce et al. (2007), and an in-house pressed pellet of the certified otolith reference powder FEBS-1 (National Research Council, Canada). The NIST 612 was analysed by continuous transects of 70 isotope scans, with 30 scans of blank gases prior to ablation. Average (%, ±SD) recovery for the NIST 612 as an unknown were (n=25); Mg: 101 ± 7, Mn 100 ± 6, Sr: 100 ± 8 and Ba: 101 ± 6. Average RSD (relative standard deviation, %) (±SD) for the NIST 612 transects was; Mg 10 ± 3, Mn 9 ± 4; Sr: 16 ± 9, Ba: 12 ± 6. For the FEBS-1 pellet average (%, ±SD) recoveries were (n=10); Mg: 120 ± 9, Mn 99 ± 17, Sr: 90 ± 6 and Ba: 113 ± 7. Average RSD for the FEBS-1 (relative standard deviation, %) (±SD) were; Mg 15 ± 3, Mn 29 ± 11; Sr: 15 ± 4, Ba: 18 ± 6. Average detection limits based on three times the standard deviation of the blank gases adjusted for ablation yield (Lahaye *et al.* 1997) were; Mg: 8.8, Mn: 0.4, Sr: 1.1 and Ba: 0.06 µmol mol^{-1}.

The profile for each element:Ca ratio was matched to fish age (i.e. yearly growth zones) using the opaque zones in the otolith macrostructure as a temporal reference (Fig. 4.2). After analysis by laser ablation ICP-MS, a digital image of the otolith was recorded from which the increment widths were measured from the core to the otolith margin adjacent to the trench left by the ablation path on the surface of the otolith section. Using these distances, the known rate of movement of the laser beam across the otolith and the time taken for individual ICP-MS scans of the isotopes, the consecutive element:Ca measurements were divided into consecutive age (years) zones. The element:Ca measurements for each age zone were then integrated to provide average element:Ca ratio data for each year of life that were used for further statistical analysis (i.e. Fowler et al. 2005).

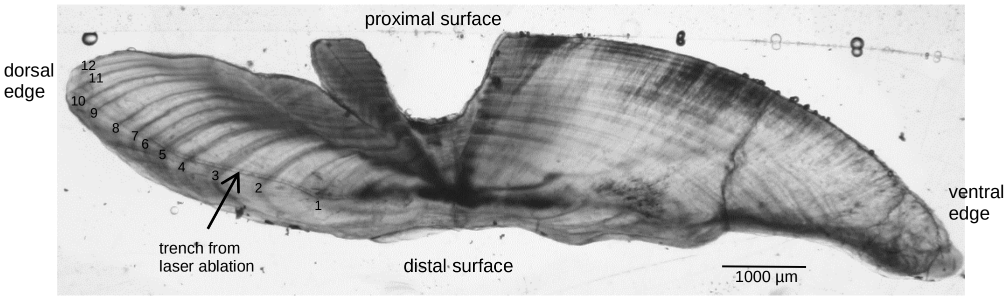

Fig. 4.2 Image of a transverse section of a snapper otolith showing the macroincremental structure. The fish was from the 1991 year class and was captured in 2003 in NSG. The opaque zones are numbered from the otolith core to its dorsal edge. The path along which chemical analysis was done is indicated by the trench left by the laser ablation. The points of intersection between this path and the opaque zones of the annual increments were used to divide the consecutive estimates of elemental concentration into annual age groupings.

4.2.4 Data analysis

As the otoliths from the four year classes were of different ages and related to different time periods, the data for each year class were analysed separately. The focus for each year class was to compare among regions for the individual ages rather than comparing between the different ages within a year class or interactions between age and region. Therefore, the regional comparisons for each age were conducted as separate analyses, as opposed to a repeated measures approach. The similarities and differences among regions for each age within each year class were used to address specific questions about regions-of-origin and changes to spatial structure with age.

To achieve these comparisons, it was necessary to simplify the transect data. For each otolith and element, an annual, age-related mean was calculated from the series of elemental concentrations that were assigned to each year. Examples of how this was done are provided in Fowler et al. (2005). The results for each otolith were profiles of age-related mean estimates of concentration of the element:Ca ratios for Ba, Sr, Mn and Mg, from all increments from the otolith core to its outside edge. These increments are labelled 0-1, 1-2, 2-3 and so on, relating to the otolith material deposited between the consecutive opaque zones from the otolith core to the outside edge.

For each year class, the among-region comparisons were achieved using analyses of variance, multivariate analyses of variance and discriminant function analyses of the age-specific annual averages. For individual element:Ca ratios and each increment (year) a single factor analysis of variance (ANOVA) was used to compare amongst regions, and a Tukey's pairwise post-hoc test was used for *a posteriori* tests to identify which regional means were significantly different. Subsequently, the data from the four element:Ca ratios were analysed with a single factor, multivariate analysis of variance (MANOVA) followed by Hotellings' T-square pairwise tests to identify which regions differed. The multi-elemental data for each increment were presented by plotting the regional 95% confidence ellipses around the mean canonical scores for canonical variates 1 and 2 from a quadratic discriminant function analysis (QDFA). Assumptions of normality and homogeneity of variances were assessed qualitatively using box plots, frequency histograms and residual plots. To meet these assumptions the data for Mn:Ca and Ba:Ca were transformed using ln(x+1). While individual variables satisfied the assumptions of the univariate analyses, assumptions of multivariate analyses are problematic to formally test (Quinn and Keough 2002). Qualitative comparisons of within-group, scatterplot matrices did not indicate major heterogeneity of within-group variance-covariances, however, quadratic discriminant functions were applied as a conservative approach as they do not assume equal within-group covariances (Quinn and Keough 2002).

4.3 Results

4.3.1 1991 year class

A total of 79 otoliths from the 1991 year class were analysed from the five regions of NSG, SSG, NGSV, SGSV and PPB (Table 4.1). The South Australian fish were sampled at 12+ years of age, whilst the Victorian ones were 9+ years of age.

Individual element:Ca ratios

The mean levels of Ba:Ca across the annual increments and regions ranged from 1.1 to 9.0 µmol mol^{-1} (Fig. 4.3a). The inter-regional comparisons were dominated by the higher concentrations recorded from the otoliths from PPB. These otoliths had a long-term increasing trend, and the concentrations were significantly higher than for the South Australian regions from the youngest to oldest increments. In contrast, the otoliths from each of the SA regions had low Ba:Ca concentrations that ranged from 1.1 to 2.6 µmol mol^{-1}, and there were no significant regional differences for any increments. Nevertheless, NSG had the lowest mean concentrations across all increments, with the mean concentrations in the otoliths from NGSV and SGSV approximately twice those of NSG for increment numbers 2-3 to 5-6.

The range of mean levels of Sr:Ca across the annual increments and regions was from 1,490 to 2,656 µmol mol^{-1}, and for all regions displayed general, non-linear increasing trends with age (Fig. 4.3b). Regional differences were apparent for several increments. For increments 0-1 and 1-2, the Sr:Ca concentrations for otoliths from PPB were lower than those for several SA regions. For the SA regions, the otoliths from NGSV had the lowest concentrations across all increments, whilst those from NSG had the highest concentrations, although differences were only significant for increments 4-5 and 5-6. The concentrations for SGSV and SSG were intermediate between these regions but the later-formed increments were more similar to the concentrations for NGSV and NSG, respectively.

The range of mean levels of Mn:Ca across the annual increments and regions was 0.3 to 10.2 µmol mol^{-1} (Fig. 4.3c). For all regions, Mn:Ca concentration declined exponentially with age. The otoliths from PPB had the highest concentrations across all annual increments, which were generally significantly higher than some, if not all, of the estimates for the South Australian regions. For the otoliths from the four South Australian regions there were no consistent differences amongst regions, although the biggest regional difference was for the 0-1 increment for which SSG and SGSV had the highest levels. However, there were no significant differences for any increments amongst the SA regions.

The Mg:Ca concentrations also declined exponentially with age (Fig. 4.3d). Generally, there were no differences in the patterns of decline amongst regions, however, for increments 0-1 and 1-2, the otoliths from PPB had significantly higher concentrations than some of the SA regions.

Multivariate analyses

For the four element:Ca ratios, the MANOVA for each annual increment identified a significant difference amongst regions (Fig. 4.4). The *a posteriori* comparisons amongst means for each increment from the otolith core to the outside edge indicated that the otoliths from PPB were significantly different from those of the South Australian fish for all annual increments (Fig. 4.4). Furthermore, there are differences between NGSV and NSG for increments 4-5 and 5-6, which are likely to relate to the regional differences in Sr:Ca concentration evident in Fig 4.2b. The regional differences are evident in the separation of the 95% confidence interval ellipses around the means in the canonical variate plots (Fig. 4.4).

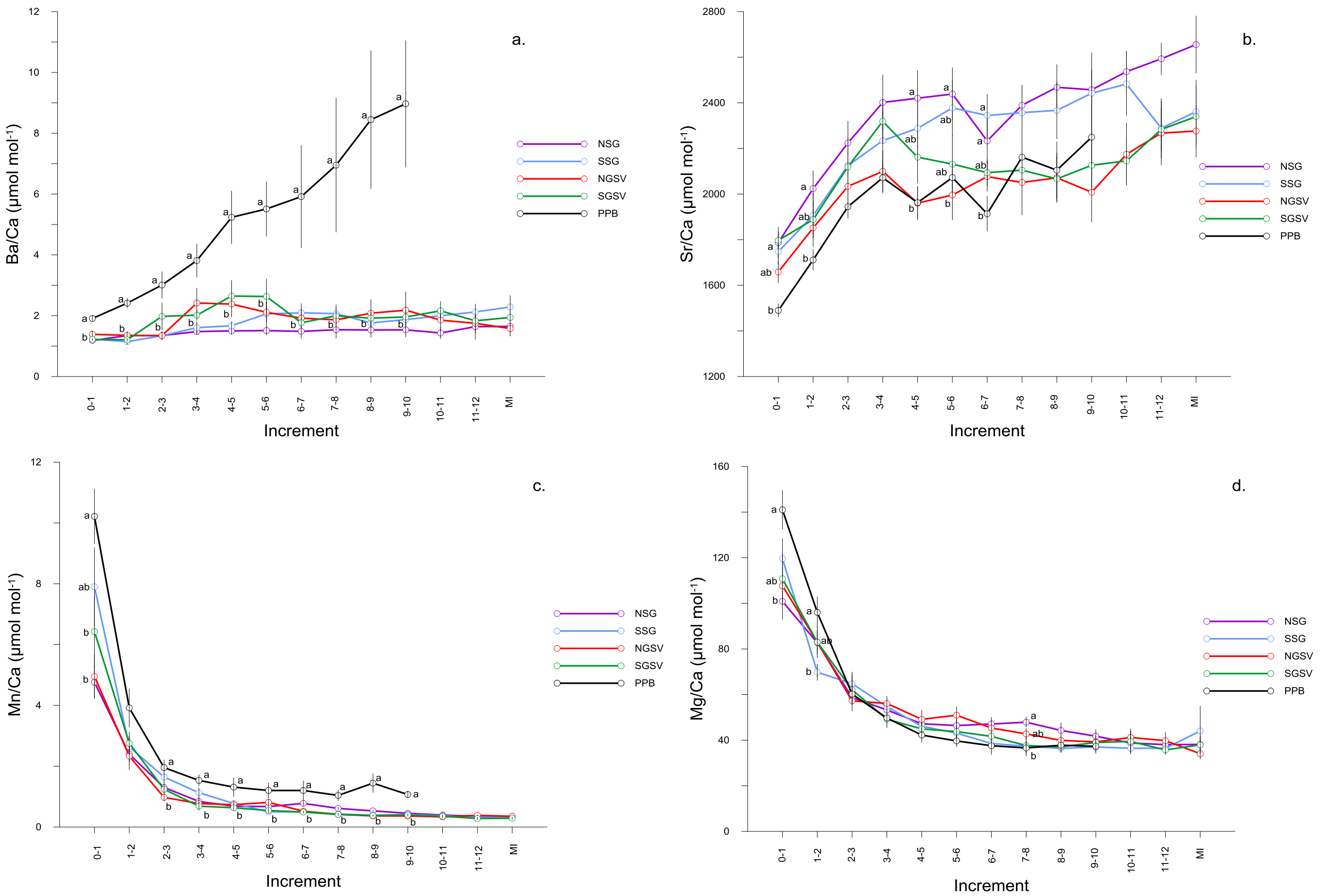

Fig. 4.3 Regional comparison of age-related element:Ca ratios across the otoliths of snapper from the 1991 year class. a. Ba:Ca concentrations. b. Sr:Ca concentrations. c. Mn:Ca concentrations. d. Mg:Ca concentrations. For each graph, the significant differences amongst regional means (Tukey's, $P<0.05$) for each increment are indicated by pronumerals (means with the same pronumeral are not significantly different, where no pronumerals are indicated for an increment there are no significant regional differences). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, PPB – Port Phillip Bay.

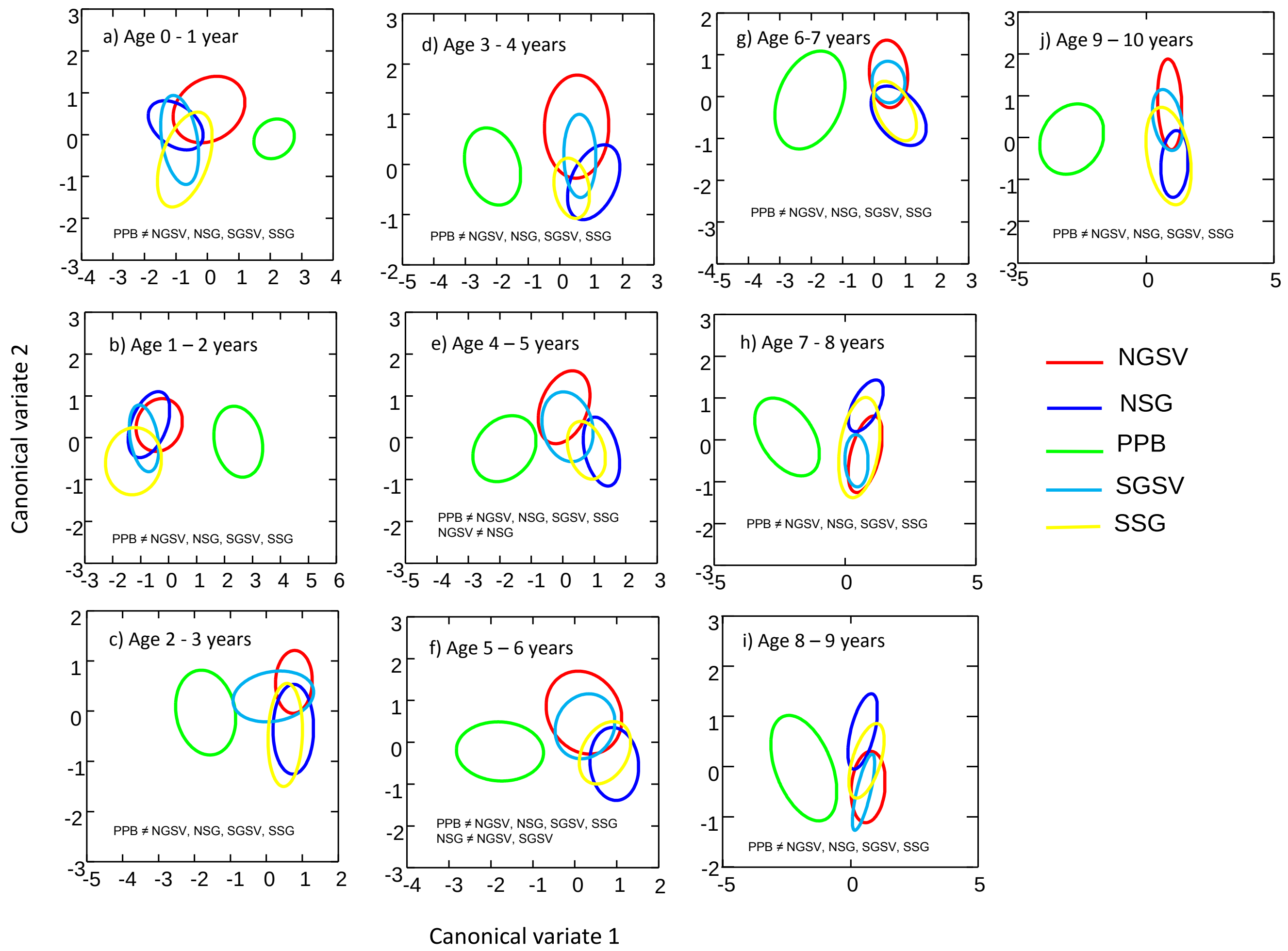

Fig. 4.4. Canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the 10 annual increments considered for the 1991 year class. Data shown in each plot are the 95% confidence ellipses around the regional means. The results of Hotellings' T-square pairwise tests subsequent to the MANOVAs are provided as text at the bottom of each plot. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

4.3.2 1997 year class

A total of 78 otoliths were considered for the 1997 year class from four South Australian regions and from PPB (Table 4.1). The South Australian fish were sampled at 11+ years of age, whilst the Victorian ones were sampled at 7+ years of age.

Individual element:Ca ratios

The range of mean estimates of Ba:Ca across annual increments and regions was 1.2 to 8.7 µmol mol^{-1}, with the age-related trends across otoliths more complex than for the 1991 year class. The otoliths from PPB consistently had Ba:Ca levels that were significantly higher than those from the four SA regions (Fig. 4.5a). For the SA otoliths, those from NGSV consistently had the lowest levels of Ba:Ca, with a notable difference between this region and NSG for increment 2-3. Furthermore, the patterns of variation were similar amongst NSG, SGSV and SSG until increment 4-5. From there, there were consistent differences in the Ba:Ca levels between the two northern gulfs (NSG, NGSV) compared to the two southern gulfs (SSG, SGSV).

The range of mean estimates of Sr:Ca across annual increments and regions was 1,598 to 2,854 µmol mol^{-1} with a non-linear increasing trend with age for each region (Fig. 4.5b). Significant inter-regional differences were only detected for a few increments, most notably, the otoliths from NGSV had the lowest mean levels of Sr:Ca for the six consecutive increments of 0-1 to 5-6, with a significant difference for increment 4-5. SSG had an elevated level of Sr:Ca at increment 6-7.

The range of mean estimates of Mn:Ca among annual increments and regions was 0.3 to 9.5 µmol mol^{-1}, and for all regions there was a declining trend with age (Fig. 4.5c). For the first few annual increments, PPB had the highest Mn:Ca, but only for increment 2-3 was this regional difference significant, with NSG having the lowest level of Mn:Ca.

Whilst the mean annual values of Mg:Ca ranged from 34.5 to 129.5 µmol mol^{-1} there was a consistent exponential decline with age (Fig. 4.5d). There were no significant regional differences for any annual increments.

Multivariate analyses

MANOVAs detected significant regional differences in otolith chemistry for each annual increment (Fig. 4.6). The results from the *a posteriori* tests identified that PPB differed from most SA regions for all increments. Furthermore, there were some notable differences for the SA regions, which from increment 2-3 onwards, related to differences between NGSV and the two Spencer Gulf regions (NSG, SSG). The bivariate plots from the canonical discriminant function analyses indicated considerable separation of NGSV from the other two regions from increment 1-2 onwards (Fig. 4.6). Ba:Ca and Sr:Ca appear to contribute most to these regional differences.

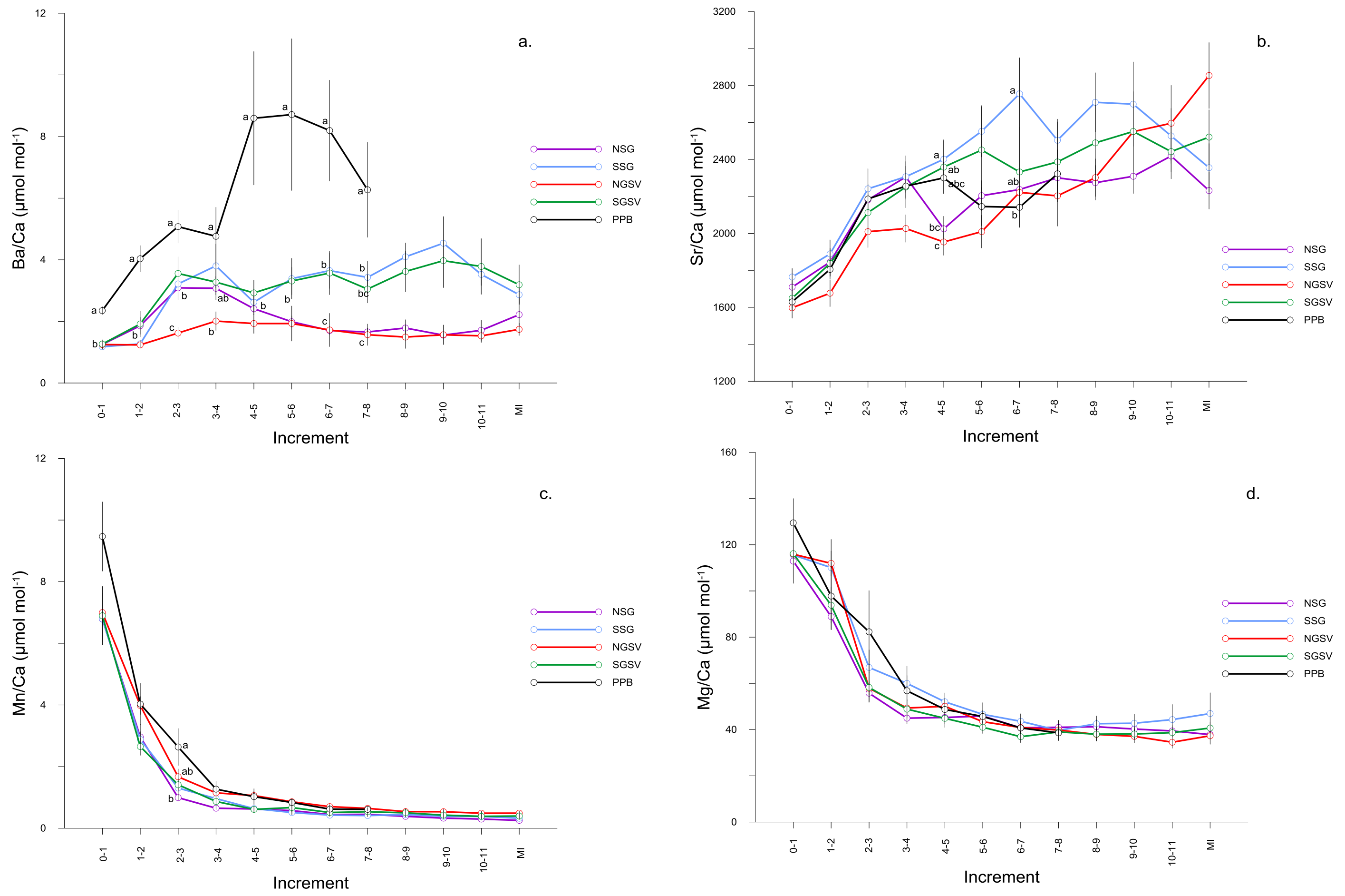

Fig. 4.5. Regional comparison of age-related element:Ca ratios across the otoliths of snapper from the 1997 year class. a. Ba:Ca concentrations. b. Sr:Ca concentrations. c. Mn:Ca concentrations. d. Mg:Ca concentrations. For each graph the significant differences amongst regional means (Tukey's, $P<0.05$) for each increment are indicated by pronumerals (means with the same pronumeral are not significantly different, where no pronumerals are indicated for an increment there are no significant regional differences). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, PPB – Port Phillip Bay.

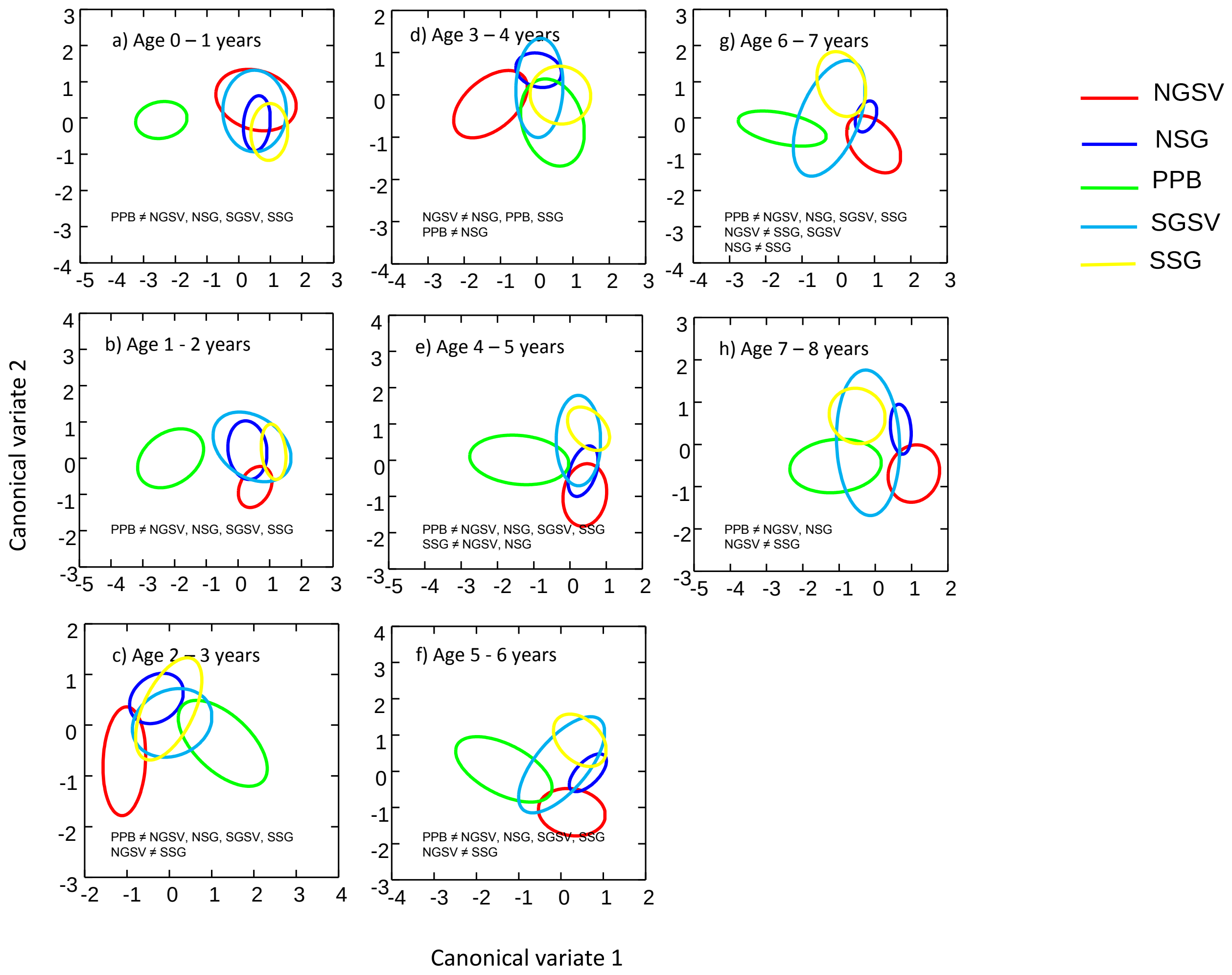

Fig. 4.6. Canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the 8 increments considered for the 1997 year class. Data shown in each plot are the 95% confidence ellipses around the regional means. The results of Hotellings' T-square pairwise tests subsequent to the MANOVAs are provided as text at the bottom of each plot. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, PPB – Port Phillip Bay.

4.3.3 2001 year class

For the 2001 year class, a total of 91 otoliths were considered, which included some from the four gulf regions and SE region of SA, and some from PPB (Table 4.1). The otoliths from the six regions were collected in 2009 and were sampled at 8+ years of age (Table 4.1).

Individual element:Ca ratios

The range of mean estimates of Ba:Ca among annual increments and regions was 1.1 to 7.0 µmol mol^{-1}. The chronological trends across the otoliths fell into several regional groups (Fig. 4.7a). Those from NSG, SSG and NGSV had Ba:Ca ratios that were low, with average concentrations generally <2 µmol mol^{-1}. For SSG there was an increase in concentration at increment number 3-4 followed by a gradual decline over subsequent increments. In contrast, the otoliths from PPB, SE and SGSV had average annual Ba:Ca ratios that were generally >4 µmol mol^{-1}. Furthermore, the patterns in variation across increments 0-1 to 3-4 for these three regions displayed considerable synchrony. However, from the 3-4 increment onwards, there were considerable differences amongst the annual estimates from PPB, SE and SGSV regions. For increments 0-1 and 1-2, there were significant differences between the two regional groups of NSG, SSG, NGSV and PPB, SE, SGSV. For subsequent increments, SSG was intermediate between the two regional groups (Fig. 4.7a).

The range of mean estimates of Sr:Ca among annual increments and regions was 1,601 to 2,847 µmol mol^{-1} with a general increasing trend with age (Fig. 4.7b). There was some age-related differentiation in Sr:Ca levels amongst regions. For increments 1-2 and 2-3, concentrations were higher for the SE, SGSV and PPB regions than for NSG, SSG and NGSV. However, from increment 4-5 onwards, there was a switch as the concentrations of Sr:Ca in the otoliths from SE, SGSV and PPB declined whilst those from the other regions continued to increase.

The range of mean estimates of Mn:Ca amongst annual increments and regions was 0.4 to 12.6 µmol mol^{-1}, with consistent exponentially declining trends with age (Fig. 4.7c). For increment 0-1, higher levels of Mn:Ca were recorded in the otoliths from PPB, SE and SGSV than from the other regions. By increments 4-5 and 5-6, some significant differences were apparent in the Mn:Ca concentrations between SE, PPB and SGSV.

The Mg:Ca concentrations across the otoliths also declined with age, with some regional differences apparent (Fig. 4.7d). For increment 0-1, the Mg:Ca levels were higher in the otoliths from the SE, SGSV and PPB than for the other regions. Alternatively for the older increments, i.e. from 4-5 onwards, the concentrations were higher in the otoliths from NSG and NGSV than from PPB, SE, SGSV regions and also SSG.

Multivariate analyses

The MANOVAs for each annual increment indicated significant regional differences in the multi-elemental otolith chemistry. The *a posteriori* tests identified numerous significant differences amongst regional means (Fig. 4.8). For each increment, these primarily reflected differences between the PPB, SE, SGSV group and the NSG, SSG and NGSV group, which are apparent in the age-related bivariate plots from the discriminant function analyses (Fig. 4.8). The region that least conformed with this geographic division in otolith chemistry is SSG, for which the multi-elemental signals for increments 3-4 and 4-5 diverged from those of the two northern gulfs and were more similar to those from the three southern regions of PPB, SE and SGSV.

4.3.4 2004 year class

For the 2004 year class, a total of 91 otoliths that were collected in 2009 from the 5+ age class were considered from the five South Australian regions and from PPB (Table 4.1).

Individual element:Ca ratios

The range of mean estimates of Ba:Ca among annual increments and regions was 1.1 to 5.5 µmol mol^{-1}, with no consistent long-term trends across the otoliths. However, there were two regional groups evident in the Ba:Ca concentrations of the first few increments (Fig. 4.9a). In contrast to 2001, the group with higher concentrations of Ba:Ca for the first few increments only involved PPB and the SE, as SGSV was grouped with NGSV, SSG, and NSG. However, after increment 2-3, these regional groupings changed considerably. The Ba:Ca concentration in the otoliths from NGSV and NSG remained low, whilst those from SSG and SGSV increased to levels comparable to those from PPB and the SE.

The range of mean estimates of Sr:Ca among annual increments and regions was 1649 to 2789 µmol mol^{-1}, and for numerous increments there were regional differences (Fig. 4.9b). For increment numbers 1-2 and 2-3, the regions divided into the same groups as for Ba:Ca, i.e. PPB and the SE had higher concentrations of Sr:Ca than the four SA gulf regions. From increment 3-4 onwards, there was a divergent trend, with the concentrations for PPB continuing to increase, whilst those for the SE region declined to the level of the four SA gulf regions.

The range of mean estimates of Mn:Ca among annual increments and regions was 0.5 to 8.7 µmol mol^{-1}, and declined exponentially with age (Fig. 4.9c). For increment 0-1, higher concentrations were recorded for the otoliths from PPB and the SE than for the four SA gulf regions (Fig. 4.9c). Subsequently, the concentrations in otoliths from PPB remained high, whilst those from the SE region declined to levels similar to the other four SA regions.

The range of mean estimates of Mg:Ca among annual increments and regions was 37.1 to 157.0 µmol mol^{-1}, and declined exponentially with age (Fig. 4.9d). There were several regional differences. For increment 0-1, the concentration for PPB was significantly greater than for

NGSV, NSG and SSG, whilst SGSV and the SE regions had intermediate levels. For each subsequent increment, the otoliths from the SE had the lowest concentrations of Mg:Ca.

Multivariate analyses

The MANOVAs that compared the multi-elemental data amongst regions for each increment identified significant differences (Fig. 4.10). For increments 0-1, 1-2 and 2-3, there were two distinct groups with the multi-elemental signal from PPB and SE similar but significantly different from those of the other four SA gulf regions (Fig. 4.10). With the later formed increments, differences emerged between some of the SA gulf regions. For the first few increments, the chemistry of the otoliths from NSG, SSG, NGSV and SGSV were very similar. However, gradually the multi-elemental signal from otoliths from SGSV diverged from those of the two northern gulfs and became more similar to those of the PPB and SE regions. The otoliths from NSG and NGSV remained similar across all increments. Those from SSG gradually diverged from those of NSG.

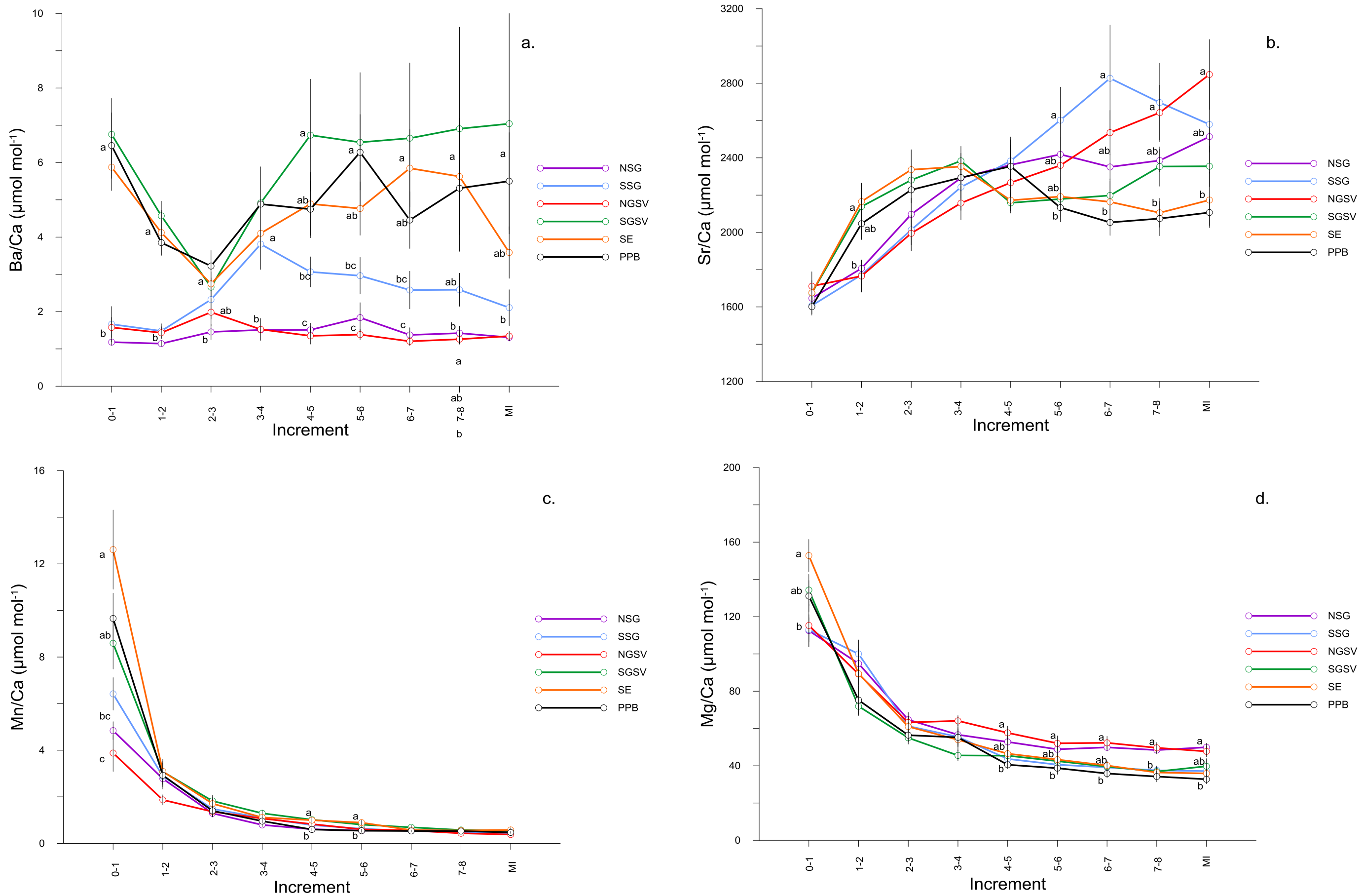

Fig. 4.7. Regional comparison of age-related element:Ca ratios across the otoliths of snapper from the 2001 year class. a. Ba:Ca concentrations. b. Sr:Ca concentrations. c. Mn:Ca concentrations. d. Mg:Ca concentrations. For each graph the significant differences amongst regional means (Tukey's, $P<0.05$) for each increment are indicated by pronumerals (means with the same pronumeral are not significantly different, where no pronumerals are indicated for an increment there are no significant regional differences). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

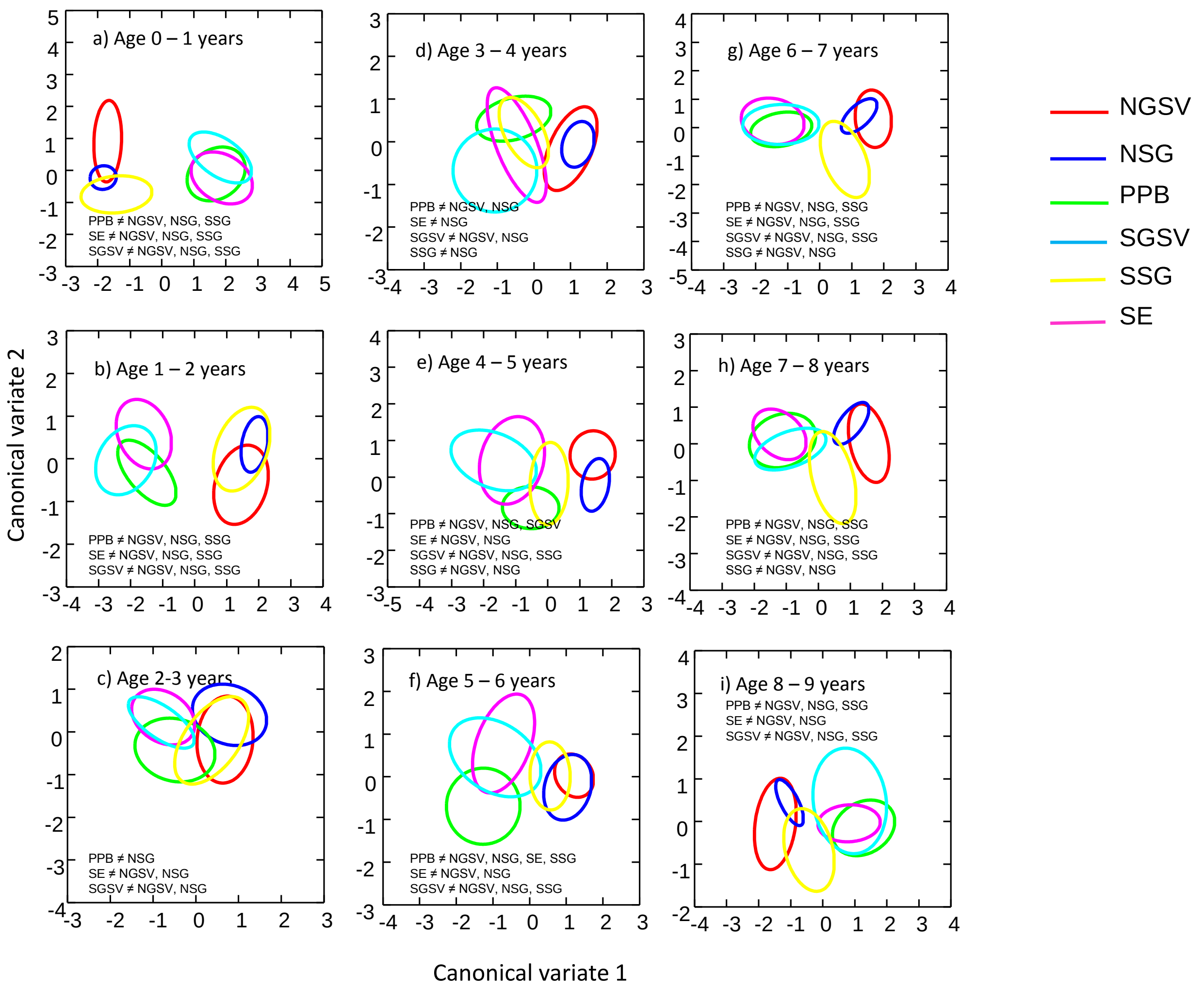

Fig. 4.8. Canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the 9 increments considered for the 2001 year class. Data shown in each plot are the 95% confidence ellipses around the regional means. The results of Hotellings' T-square pairwise tests subsequent to the MANOVAs are provided as text at the bottom of each plot. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

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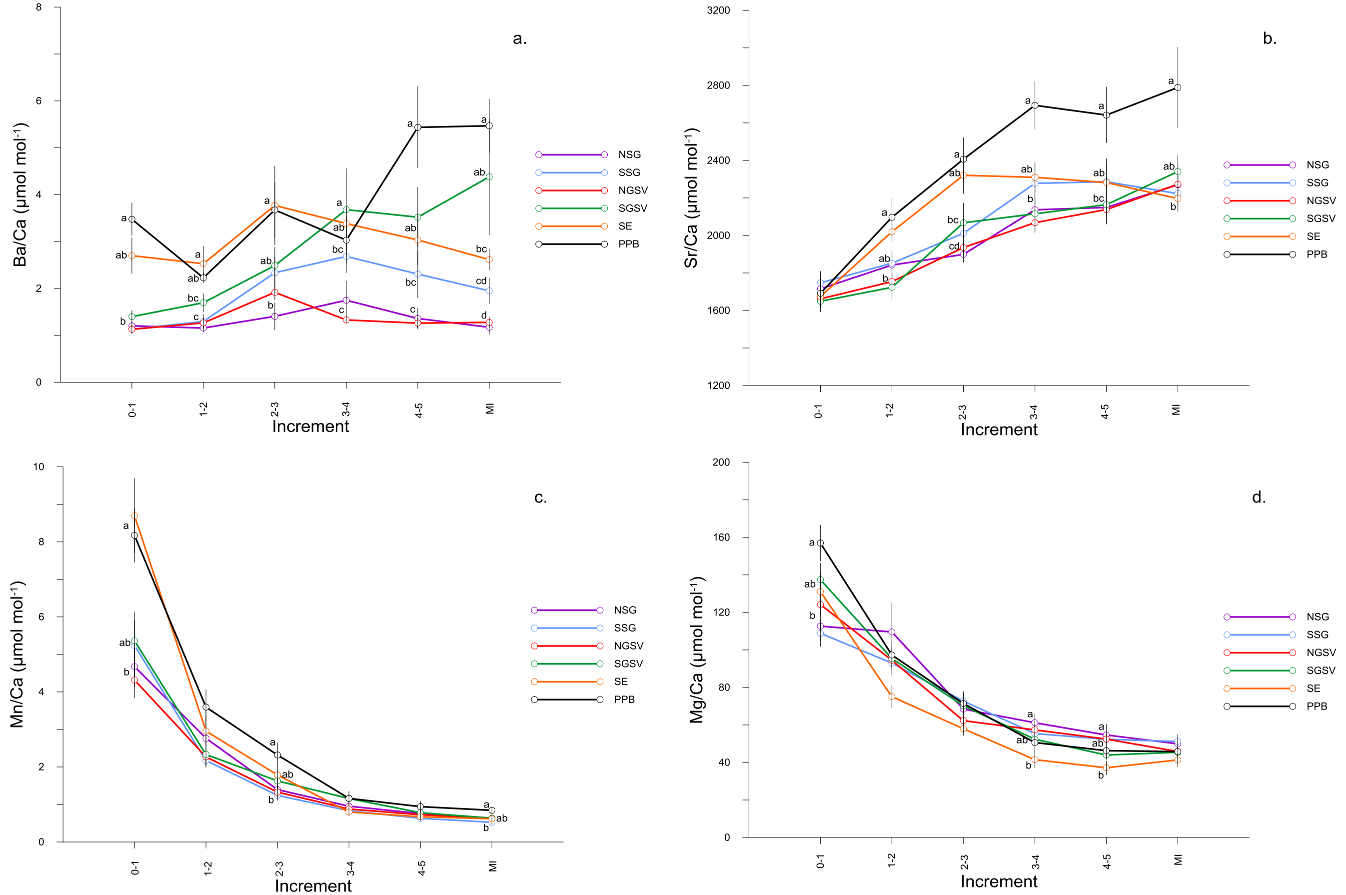


Fig. 4.9. Regional comparison of age-related element:Ca ratios across the otoliths of snapper from the 2004 year class. a. Ba:Ca concentrations. b. Sr:Ca concentrations. c. Mn:Ca concentrations. d. Mg:Ca concentrations. For each graph the significant differences amongst regional means (Tukey's, $P<0.05$) for each increment are indicated by pronumerals (means with the same pronumeral are not significantly different, where no pronumerals are indicated for an increment there are no significant regional differences). NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

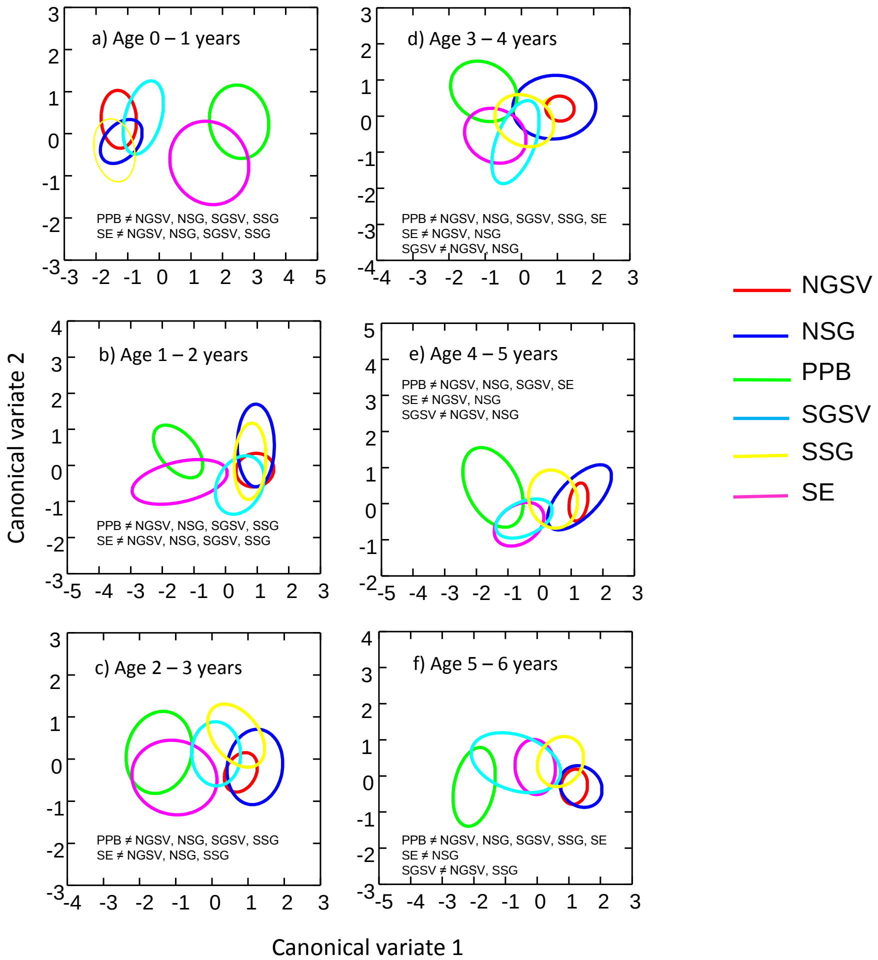


Fig. 4.10. Canonical variate plots from the discriminant function analyses for the multi-elemental datasets for each of the 6 increments considered for the 2004 year class. Data shown in each plot are the 95% confidence ellipses around the regional means. The results of Hotellings' T-square pairwise tests subsequent to the MANOVAs are provided as text at the bottom of each plot. NSG – Northern Spencer Gulf, SSG – Southern Spencer Gulf, NGSV – Northern Gulf St. Vincent, SGSV – Southern Gulf St. Vincent, SE – South East, PPB – Port Phillip Bay.

4.4 Discussion

4.4.1 Regional comparisons of otolith chemistry

In this study, the elemental analysis of otoliths of snapper from south eastern Australia showed that Sr, Ba, Mn and Mg were incorporated into the $CaCO_3$ crystalline structure as impurities, and that these elements were evident across the chronological structure of otoliths at concentrations above the limits of reliable detection by laser ablation ICPMS. The average annual concentrations for Sr:Ca of approximately 1500 – 3000 µmol mol^{-1} were substantially higher than those for Mg (40 – 150 µmol mol^{-1}), whilst those for Ba:Ca and Mn:Ca were approximately one order of magnitude less again (1.0 – 10 µmol mol^{-1}). The age-related regional patterns varied across the annual increments of the otoliths. Except for PPB, the Ba:Ca concentrations across the otoliths were relatively flat, showing no long-term relationships with age. Alternatively, for each of Sr:Ca, Mn:Ca and Mg:Ca there were long-term ontogenetic patterns that were generally consistent amongst regions. Whilst the concentrations of Sr:Ca generally increased with age, in complex and nonlinear ways, those for Mn:Ca and Mg:Ca decreased exponentially across the otoliths. Despite these long-term, ontogenetic patterns, the comparison of the single element profiles and multi-elemental data demonstrated significant spatial and temporal differences. Such differences can be used to infer spatial and temporal connectivity among regional populations and to address questions about the processes of regional population replenishment and demography. Below we address key questions for each of the major fishery regions in SA.

South East Regional Population

The population of snapper in the SE region of SA experienced a dramatic increase in biomass that led to unprecedented fishery catches from 2007 to 2013 (Chapter 1 this report, Fowler et al. 2013). Prior to 2007 there was only a minor commercial catch from this region. The fundamental questions about these regional population changes are – where did these fish come from and when did they arrive? The expectation is that the fish must have moved to this region from elsewhere, as there is no known snapper nursery area within this region capable of producing sufficient numbers to support such a large and rapid increase in biomass and fishery catch. Although snapper are likely to spawn in coastal waters and large bays and gulfs, their important nursery areas are typically, large, protected embayments and gulfs (western Victoria, SA, WA and New Zealand), as well as in estuaries (i.e. eastern Victorian/NSW) (Francis 1995, Fowler and Jennings 2003, Hamer and Jenkins 2004, Wakefield 2010, Dias et al. 2015). The three primary nursery areas for south eastern Australia that could potentially be the source areas that supply the recruits to each of the South Australian regional populations including the SE are NSG and NGSV (Fowler and Jennings 2003, Fowler et al. 2005) and PPB (Hamer and Jenkins 2004, Hamer et al. 2006).

For the SE region, otoliths were only available for elemental analysis for the 2001 and 2004 year classes due to low commercial catches prior to 2007. For both year classes, the elemental concentrations for the first few increments, representing the juvenile phase of the life cycle, were very similar to those from PPB. They had elevated levels of Ba:Ca, which previous studies have demonstrated to be a strong indicator for PPB (Hamer et al. 2005, 2006, 2011). Furthermore, the otoliths from both regions had higher concentrations of Sr:Ca, Mn:Ca and Mg:Ca than did the first few increments in the otoliths from NSG and NGSV. These results and lack of evidence for major spawning and nursery areas in south-east SA coastal waters, support the hypothesis that the SE snapper originated in PPB.

The chemistry across the otoliths from the SE and PPB diverged from the 1-2 increment onwards, with the differences particularly strong for the 4-5 and 5-6 increments. This divergence is consistent with the SE fish leaving PPB and moving the 600 km westward through the western Victorian coastal waters to end up in the regional waters of south eastern South Australia. The divergence of otolith chemistries from the 1-2 increment onwards, suggests that some fish left PPB as juveniles, as documented in previous studies (Coutin et al. 2003, Hamer et al. 2006). However, the divergence over several annual increments suggests that all emigrants from PPB did not leave the bay at the same time but rather their departures were staggered over a few years. The higher fishery catches from the SE were evident in the wholesale fish market in Adelaide at least in 2007, and consisted primarily of the 6+ aged fish from the 2001 year class (Fowler et al. 2010). The 2004 year class became evident in the SA market in 2009, when the fish were in the 5+ age class. As such, it may have taken several years for the fish to complete the long, westward journey from PPB to the SE.

A key observation that supports the conclusion that snapper from the SE region were derived from spawning in PPB was that annual research surveys of small 0+ year class (<6 months old, 3-10 cm CFL) undertaken in PPB, showed that the highest recruitment events that occurred in the last 23 years were in 2001 and 2004 (Kemp et al. 2011). Furthermore, over the four year period of 2008 to 2011, the SE population produced 556 t of commercial catch of snapper that was dominated by fish from the 2001 and 2004 year classes (Fowler et al. 2013). These fish were generally small for their ages and weighed only a few kg. Consequently, to support such a gross catch there must have been large numbers of snapper that originated in PPB in 2001 and 2004 and subsequently emigrated to the regional waters off south eastern South Australia.

Southern Gulf St. Vincent Regional Population

The annual catches of snapper from SGSV have historically been relatively low and not made a major contribution to SA's catch, suggesting a consistently low fishable biomass. The annual catches increased from 2009 to 2012, although the scale of the increase was small compared to those in NGSV and the SE (Chapter 1 this report, Fowler et al. 2013). The primary demographic questions for this region are – from where was this regional population replenished, and was this consistent amongst year classes? To address this question, the chemistries of otoliths from the four year classes of 1991, 1997, 2001 and 2004 were considered.

For the 2001 year class, the elemental concentrations for the first three years of the fish's lives were almost identical to those from PPB and the SE but contrasted with the low levels of Ba:Ca, Sr:Ca, and Mn:Ca in the otoliths from fish from NSG and NGSV. The obvious conclusion from these overwhelming results is that the fish from the 2001 year class that were captured in 2009 from SGSV had also originated in PPB. This would require that they had moved a greater distance westward than the fish captured in the SE. The lower abundance in SGSV reflected that fewer fish achieved this greater distance of travel, and may indicate the limit of their westward extent.

For the 2004 year class, the chemistry of the first formed increments in the otoliths from SGSV differed considerably from those from PPB and the SE. The low levels of Ba:Ca, Sr:Ca and Mn:Ca were more similar to concentrations in the otoliths from NSG and NGSV. These data strongly suggest that the 2004 year class of snapper sampled from SGSV did not originate in PPB, but came from either NSG or NGSV, and that movement from either nursery area towards SGSV commenced during the second or third year of life. Note that the SGSV fish sampled from both the 2001 and 2004 year classes mostly came from the same location near Cape Jervis in Investigator Strait (Fig. 4.1), which indicates that sample location did not account for the likely different origins between the two year classes.

For the 1991 and 1997 year classes, the individual element:Ca profiles and multi-elemental data for the first few increments differed from those from PPB, as occurred for the 2004 year-class. This eliminates PPB as the replenishment source for this region for these two year classes. For the 1991 year class, there were no apparent differences in otolith chemistry for the first few annual increments between otoliths from SGSV compared with those from NSG and NGSV, making it difficult to differentiate between these two regions as the source population for SGSV. For the 1997 year class, the elemental profiles for SGSV were more similar to those from NSG than from NGSV, with the canonical variate plots overlapping little between NGSV and SGSV from increment 1-2 onwards, but with considerable overlap apparent between NSG and SGSV. It is therefore tempting to propose NSG as the source population for the 1997 year class in SGSV. To support this contention, from 1999 to 2002, the adult biomass and therefore the potential for egg production and source of recruits was at a record level in NSG, compared to a much lower level in NGSV (Fowler et al. 2013).

Southern Spencer Gulf Regional Population

For SSG, otoliths were available from the four year classes of 1991, 1997, 2001 and 2004. The chemistry data from these were used to address the primary demographic question – from where was this regional population replenished? For each year class there were sufficient differences in otolith chemistry across all increments compared with those from PPB to eliminate the latter as a source of replenishment for SSG.

For the 1991 year class, there were no significant differences across the otoliths from SSG compared with either NSG or NGSV. In contrast, for the 1997 year class, the trends in elemental profiles for Ba:Ca, Sr:Ca and Mn:Ca for SSG and NGSV diverged from increment 1-2 onwards, producing significant differences from increment 3-4. These diverging trends in otolith chemistry from the 2+ age class onwards, the relatively higher biomass of snapper in NSG in 1997, and the proximity and geographic continuity between NSG and SSG suggest the likelihood that recruitment to the latter region came from NSG.

For the 2001 year class, there were no differences in chemistry for the first few increments between the otoliths from SSG and those from NSG and NGSV, providing no clear signal that differentiated SSG fish from either potential source population. The Ba:Ca concentration for SSG diverged after the 2-3 increment onwards, suggesting that movement of the fish occurred during their 4^{th} year, i.e. during 2004. The high biomass of snapper in NSG in 2001 and therefore potential for egg production suggests that this was the likely source population for the 2001 year class. The latter was relatively strong in NSG, which could have caused considerable density dependent pressure for such fish to migrate southwards from NSG.

By comparing the chemistry of the otoliths from SSG with those from both NGSV and NSG for the 2004 year class revealed no significant differences for the first few increments. As such, it is not possible to draw inferences about the origin of the 2004 year class in SSG.

Northern Gulf St. Vincent regional population

One of the most significant objectives of this study was to determine the processes responsible for the build-up in biomass of snapper in NGSV that led to the record commercial catches from 2008 onwards, particularly from 2010 (Chapter 1 this report, Fowler et al. 2013). Given that NGSV is one of the primary nursery areas of south eastern Australia (Fowler et al. 2004, 2005b), the biomass may have gradually accumulated through local demographic processes of reproduction and recruitment. Alternatively, snapper may have moved here from elsewhere.

Otolith chemistry data are available for NGSV for each of the 1991, 1997, 2001 and 2004 year classes. For each year class there are significant differences compared with the chemistry of otoliths from PPB. This includes the 2001 year class for which it was apparent that fish from PPB had made it as far west as SGSV, which is only 120 km to the south of NGSV. The clear differences in otolith chemistry between NGSV and PPB exclude the latter as a source of replenishment of the population in NGSV. This leaves the possibilities that the biomass in NGSV either built up through local reproduction and recruitment or fish migrated from NSG.

For each of the 2001 and 2004 year classes, the elemental profiles from NSG and NGSV were similar and no differences were apparent across the otoliths. In the context of stock discrimination, such similarities in otolith chemistry are not particularly informative (Campana 1999). This is because such similarity could reflect different scenarios of stock separation: it could indicate that the fish from different regions originated from the same source population; or that the fish originated in different places that had similar physico-chemical environments that produced otoliths with similar elemental fingerprints. As NSG and NGSV are both inverse estuaries with similar regimes of water temperature and salinity, with minimal freshwater input, the physico-chemical environments they offer to the fish are likely to be very similar (Nunes and Lennon 1986, de Silva Samarasinghe and Lennon 1987). Therefore, the similarity in the chemistry of the otoliths for these three year classes does not help to differentiate between the two alternative hypotheses regarding the population replenishment of NGSV.

Compared to the 2001 and 2004 year classes, there were subtle differences in otolith chemistry between NSG and NGSV for the 1991 and 1997 year classes. The NGSV otoliths from the 1991 year class had consistently higher concentrations of Ba:Ca, but lower concentrations of Sr:Ca than did those from NSG. For the 1997 year class, the annual estimates of Ba:Ca concentration in the otoliths from NGSV were consistently low, the concentrations in the otoliths from NSG were considerably higher for the 1-2, 2-3 and 3-4 increments. Also, the otoliths from NGSV had lower levels of Sr:Ca and higher levels of Mn:Ca for the early formed increments. As such, there were regional differences for the 1-2, 2-3 and 3-4 increments. Whilst for this year class none of the single-element data were statistically significant, possibly reflecting an issue of statistical power, there were regional multivariate differences for several increments. These differences indicate that if fish from the 11+ age class sampled in NGSV in 2008 had originated in NSG, they must have migrated between the gulfs prior to formation of most of the 1-2 increment. As most annual growth of snapper otoliths occurs during summer and autumn (Fowler and Schilling 2004), the 1-2 increment would largely have formed during their second summer. Therefore, these fish would have had to have moved from NSG to NGSV during their first year of life. Given that 0+ fish generally only reach about 15-20 cm CFL in their first year, it is unlikely that such fish would have undertaken a journey over distances of hundreds of kilometres across several ecosystems. Furthermore, such a journey would require them to move through SSG, Investigator Strait and SGSV, without mixing with the population that was sampled in these regions. Their otolith chemistry data showed no indication of this occurring because apart from the 1991 year class, the NGSV and SGSV samples showed different chemistry.

The relatively subtle differences in otolith chemistry between NGSV and those from Spencer Gulf for the 1991 and 1997 year classes suggest that the fish originated from different nursery areas. This would suggest that at least these two year classes of snapper in NGSV did not eventuate from immigration from elsewhere, but resulted from local reproduction and recruitment.

4.4.2 Conclusions

Overall, the otolith chemistry data indicated three key processes of regional population replenishment. Firstly, the strong 2001 and 2004 year classes in PPB resulted in greater levels of dispersal of snapper from Victorian waters into SA that reached as far east as Cape Jervis in SGSV. This process of stock expansion means that the western boundary of the Western Victorian Stock of snapper, typically referred to as being at near the Murray River mouth, is not a fixed boundary and may expand west or contract east depending on year class strength in Port Phillip Bay. The fishery off the SE of SA is therefore periodic, reflecting temporally variable recruitment. Secondly, the southern gulf regions are likely to depend on multiple sources of replenishment. The principle source for SSG is NSG. Alternatively, for SGSV, the contributions from NSG, NGSV and PPB are likely to vary in significance over time. Thirdly, although the data are less conclusive, there was no strong evidence to suggest that replenishment of NGSV was dependent on NSG or vice-versa, supporting the hypothesis that each is a self-replenishing, regional population.

5. Acoustic telemetry

Anthony Fowler, Charlie Huveneers, Matthew Lloyd

5.1 Introduction

The dispersion of the individuals of an animal species in space and time directly 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 population densities, dynamics and genetics as well as species evolution (Brown and Orians 1970). Furthermore, it contributes to understanding ecosystem structure and functionality, which can have practical significance for designing spatial management systems for fishery management and/or conservation purposes. For example, useful marine reserves must be of a size and habitat configuration commensurate with the mobility and resource requirements of ecologically 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. It has an extensive geographic range throughout which populations are dispersed across broad depth ranges and throughout a diversity of habitats (Kailola et al. 1993). Nevertheless, individual fish can demonstrate habitat preferences in their space use, with juveniles and adults being thigmotaxic, at times forming large aggregations around structures and features in natural habitat and artificial reefs (Fowler et al. 2013). Furthermore, snapper is a large, carnivorous, demersal species that can be of sufficient abundance to impact on the numbers and biomass of their preferred benthic prey taxa that include crustaceans, molluscs and other fish species (Lloyd 2010).

Studies on snapper movement have been done since the 1960s. Some studies used tag/recapture techniques (Paul, 1967, Sanders 1974, Crossland 1976, Jones 1981, 1984, Moran et al. 2003, Sumpton et al. 2003, McGlennon 2004, Norriss et al. 2012), whilst recent studies 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). The numerous tag/recapture studies demonstrated that at different places snapper showed specialised, idiosyncratic migratory patterns (Moran et al. 2003). Furthermore, most studies have 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 (2004) differentiated such alternative movement behaviours into ‘residents’ and ‘migrants’. This generalisation from the tagging studies implies that most snapper do not move far relative to their capabilities for movement. This is supported by findings from a number of local-scale 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 limited areas (Kingett and Choat 1981, Willis et al. 2001, Parsons et al 2003, Egli and Babcock 2004, Parsons et al. 2010). As similar local studies have not yet been done for Australian populations of snapper, there is currently a better understanding of large-scale movement over distances of 100s of km than there is for local movement over distances of metres to km. This is paradoxical as it is the more numerous 'resident' fish (McGlennon 2004), about which we have the least understanding.

The snapper fishery of South Australia has undergone significant change over the past decade. Commercial catches increased to record levels between 2008 and 2011, largely based on a significant change in the spatial structure of the fishery (Fowler et al. 2013). In particular, there was a considerable increase in biomass of snapper in Northern Gulf St. Vincent (NGSV), which has now become the mainstay of South Australia's snapper fishery. Given the current significance of this regional commercial fishery, the management focus has been to ensure its long-term sustainability. Nevertheless, identifying the best management strategy to achieve this has been challenging because of limited understanding of the processes that led to the substantial increase in biomass in NGSV and the behaviour of snapper throughout the region with respect to their movement, residence, and their habitat and resource use. The purpose of this chapter was to address the latter shortcoming by investigating the within-region movement behaviour of snapper throughout NGSV to inform the development of management strategies. Furthermore, it was considered that the study may contribute to the findings of Chapters 2 to 4 of this report by providing insight to the influence of movement on population dynamics and the relationship between the NGSV regional population and the South Australian Stock.

The study used acoustic telemetry to describe the movement behaviour of snapper at the spatial scale of km to 10s of km. This scale is substantially smaller than the large, inter-regional scale considered using the indirect 'otolith' methods described in Chapters 3 and 4. Over the past 20 years, acoustic telemetry has become an important method for studying fish movement behaviour (Clements et al. 2005, Heupel et al. 2006, How and de Lestang 2012). It involves the complementary use of acoustic transmitters and receivers to provide presence data through time at specific locations, after which the sequence of detections can be interpreted as fish behaviour in terms of movement, site fidelity, and periods of occupancy (Heupel and Webber 2012). An acoustic tag is a coded transmitter that emits series of pings which represent pulse trains of data that include an identification code, date and time of day and possibly also water temperature and depth, depending on tag type. The electronics and battery of the tag are embedded in epoxy that is moulded to a cylindrical shape for easy insertion into the fish. The acoustic receiver is a submerged monitor housing an omni-directional hydrophone that records the pings from nearby acoustic transmitters that are then stored autonomously by a data logger. Acoustic telemetry has been successfully used to address many different types of questions in relation to movement behaviour and its implications for a large range of aquatic taxa including chondrichthyans, crustaceans, cephalopods and teleost fishes at a range of spatial and temporal scales in different aquatic environments (Zeller 1998, Comeau et al. 2002, Simpfendorfer et al. 2002, Heupel et al. 2006, Heupel and Webber 2012).

The specific objectives addressed in this study for snapper in NGSV were to:

1. assess the tractability of using acoustic telemetry to study movement behaviour;
2. describe behaviour at daily, seasonal and annual temporal scales;
    a. in terms of the locations and habitats occupied at different times;
    b. and in terms of distances moved, and their timing and locations;
3. interpret movement in terms of the stock structure and contribute to determining the appropriate spatial scale for managing South Australia's snapper fishery.

The specific null model tested had evolved from earlier acoustic telemetry studies on snapper movement in New Zealand (Hartill et al. 2003, Parsons et al. 2003, 2010, Egli and Babcock 2004), where individuals typically exhibited strong site fidelity and had long periods of occupancy of restricted home ranges that involved only one or two centres of activity.

5.2 Methods

5.2.1 Study site

The study site was located in the northern part of Gulf St. Vincent (NGSV). This gulf is a large, north-south oriented, marine embayment of 120 km length, located in the central part of southern Australia's temperate coastline (Shepherd et al. 2008) (Fig. 5.1). Kangaroo Island (KI) is located across the mouth of the gulf which restricts exchange with the ocean, leading to long residence times of water in the gulf (de Silva Samarasinghe and Lennon 1987). Furthermore, KI restricts the oceanic swell, resulting in the gulf being a relatively low-energy environment, particularly in the north (Tanner 2005). The gulf is relatively shallow with a mean depth of 21 m, is deepest at 40 m in the south and becomes progressively shallower in the north (Tanner 2005). Furthermore, it is saucer-shaped, i.e. shallower at the coastal margins dropping to a deeper channel that runs to the north closer to the western side. The gulf is an inverse estuary, i.e. salinity increases from the mouth northwards due to low precipitation, low terrestrial input of freshwater and high evaporation rates (de Silva Samarasinghe and Lennon 1987). The northern part of the gulf is triangular in shape, narrowing towards its apex (Fig. 5.1). The benthic habitat is dominated by soft sediments that support extensive seagrass meadows that are dominated by *Posidonia* spp. Heading north towards Black Point, the deeper channel supports an ascidian/bryozoan assemblage, which gives way to a *Pinna*-holothurian assemblage (Tanner 2005). The habitat in this region has experienced less degradation since the 1960s compared to the south, possibly due to the low terrestrial run-off and history of only a low level of prawn-trawling (Tanner 2005).

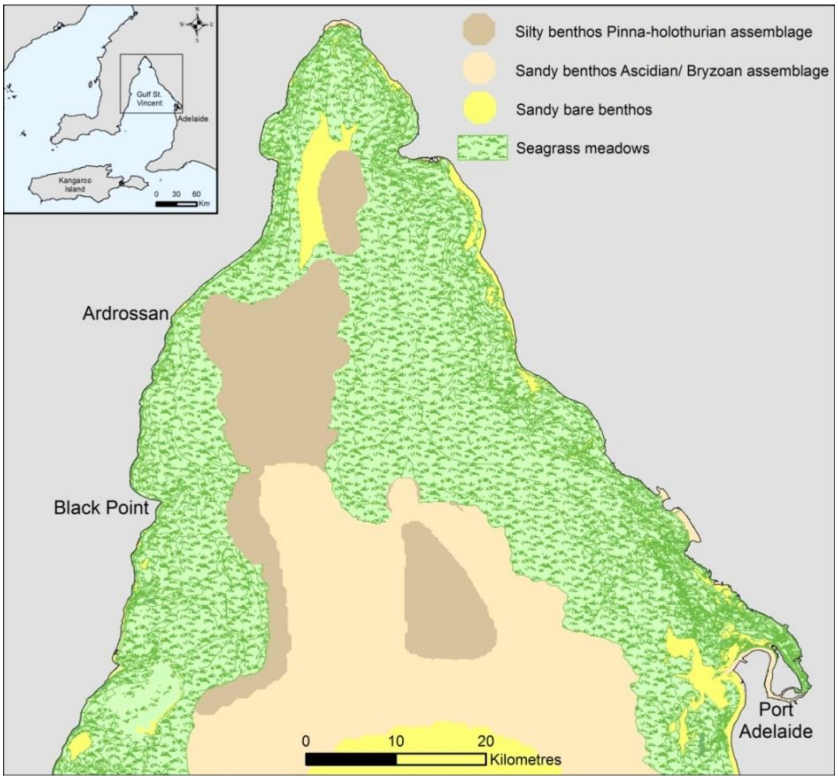


Fig. 5.1 Map of Northern Gulf St. Vincent showing the benthic habitats throughout the region. Inset shows the large-scale map which indicates the relative locations of Gulf St. Vincent and Kangaroo Island.

5.2.2 Acoustic receiver deployment

The research project ran for approximately three years from late May 2011. At that time an array of VR2W Vemco acoustic receivers was established in a study area that involved six contiguous smaller component areas (AN, AR, AG, ZN, BP and LS), largely based on habitat and bathymetry (Fig. 5.2). The number of receivers and configuration of the array were modified marginally from year to year (Table 5.1), and the areas of seafloor within which the receivers were distributed were approximately 150–160 km^2. The array of receivers in NGSV augmented 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. 5.2a). Over the three years, these lines of receivers were maintained at the Outer Channel of Port Adelaide (PG1 – PG4), at Semaphore (SE1 – SE5) and Glenelg (GL1 – GL10), whilst between years they were switched from Grange (GR1, GR2) and the mouth of the Torrens River (TM1 – TM4) to Aldinga (AL1 – AL7). The number of receivers deployed throughout the gulf ranged from 50 to 67 (Table 5.1).

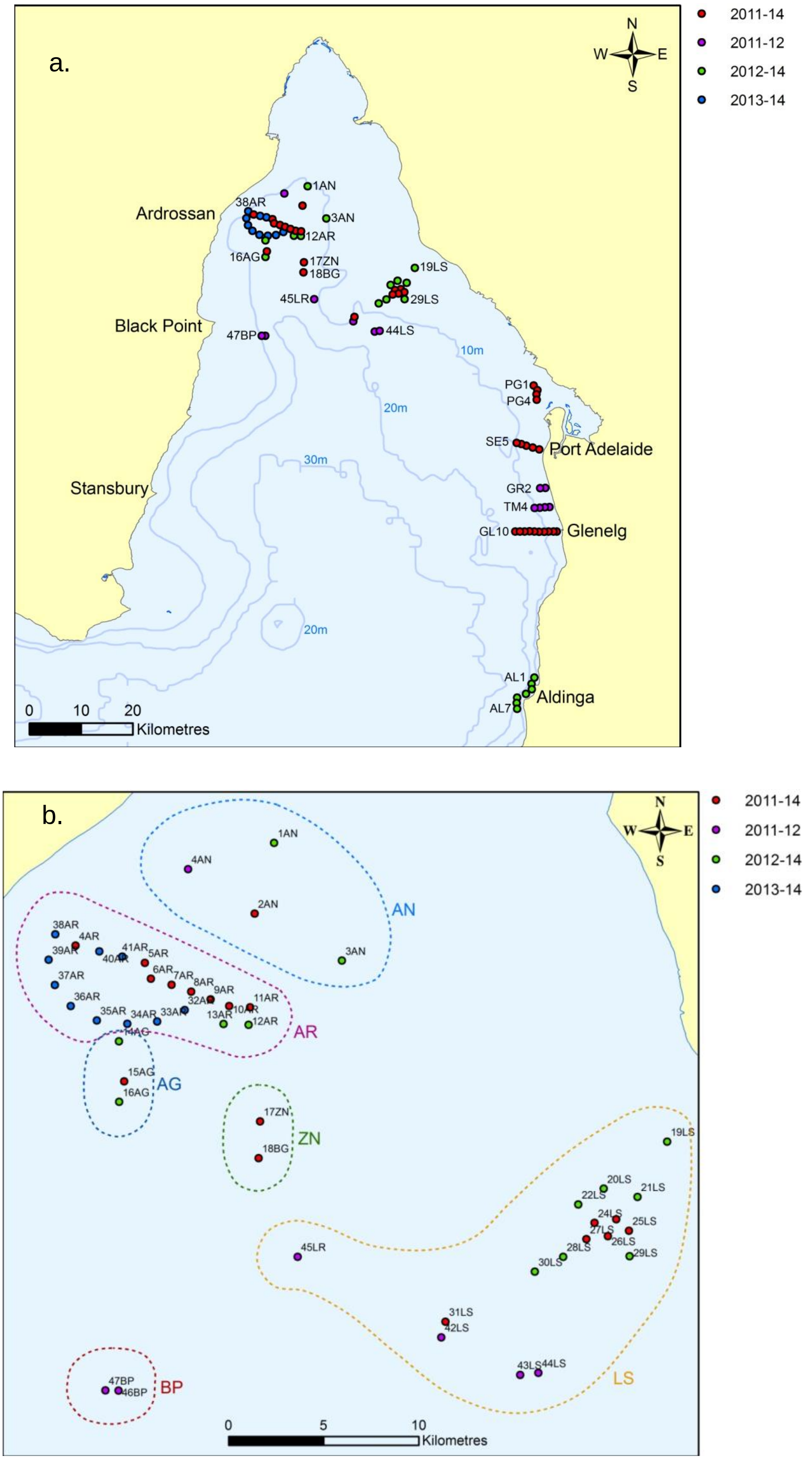


Fig. 5.2 Maps showing the configuration of acoustic receivers deployed throughout the three years of the acoustic telemetry study for snapper. a. Map of Gulf St. Vincent showing the array of receivers in the northern gulf and lines of receivers along the metropolitan coastline. Depth contours are indicated. 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.

Over several days from 17th May 2011, acoustic receivers were deployed strategically at stations between Black Point and Ardrossan in the west, across to the eastern side of the gulf. Stations for deployment throughout the six areas were selected on the advice of commercial fishers and included habitats of small natural and artificial reefs, mussel beds, *Pinna* beds and seagrass meadows (Tables 5.1, 5.2; Figs. 5.1, 5.2a). 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). As this shipwreck has considerable heritage value, a strategy for protecting it from damage from anchors of fishing boats was implemented in 1984 when a barge of 39.9 m in length was sunk one nautical mile to its south as an alternative place for fishing. An acoustic telemetry listening station (18BG) was established at this latter site.

Each acoustic receiver was deployed by attaching to a star picket that had been driven into the sea floor or was embedded in a concrete mooring that was lowered to the seabed. The receiver was positioned vertically approximately 0.5-1 m above the seabed, with the hydrophone located above the star picket. The GPS coordinates of each station were recorded.

Table 5.1 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. 5.2.

Detection period	Area						NGSV – total	GSV – total
	BP	AN	AR	AG	ZN	LS		
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

In April 2012, during the first retrieval of data from the acoustic receivers, considerable modifications were made to the configuration of the array for the subsequent detection period of April 2012 to May 2013 (Table 5.2, Fig. 5.2b). Whilst six more receivers were added, one receiver was missing, and others were removed from several stations because of low detection numbers or logistic issues relating to water depth (Table 5.2, Fig. 5.2b). For the last detection period of May 2013 to July 2014, the same configuration of receivers was maintained as for 2012/13, although with the addition of a further 10 receivers that were deployed in July 2013 in area 'AR' (Table 5.2, Fig. 5.2b). In total, 18 stations were maintained across the three years, 13 were maintained for two years, whilst 10 stations were established for only the last year of the study (Fig. 5.2b).

Table 5.2 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

5.2.3 Acoustic tagging

Two main sizes of coded transmitter tags were used i.e. V13 and V16 tags (Vemco Ltd, Nova Scotia, Canada). The different tags varied in their physical dimensions according to battery type, power level, and presence/absence of a pressure sensor for recording water depth (Table 5.3). Each tag transmitted the acoustic pings at 69 kHz at random intervals within specific ranges to reduce the likelihood of code collisions that could reduce the detection rate and increase the possibility of false detections. The ping train included an identification number specific to the tag. Life spans of tags varied according to battery size, power level, and tag capabilities (Table 5.3).

Table 5.3 Summary of characteristics of acoustic tags used in the acoustic telemetry study for snapper in NGSV.

Tag type	Tag width (mm)	Tag length (mm)	Weight in air (g)	Pressure sensor	Nominal delay (seconds)	Estimated tag life (days)
V13-1L	13	36	11	-	40-80	623
V13-1L	13	36	11	-	50-100	754
V13P-1L	13	48	13	Y	40-80	399
V13P-1L	13	48	13	Y	80-160	727
V16-4H	16	68	24	-	40-80	863
V16-5H	16	68	36	-	40-80	484
V16P-4H	16	71	26	Y	40-100	774
V16-6H	16	95	34	-	50-110	2,116

Between 26 May 2011 and 23 May 2014, 17 night-time fishing operations resulted in successful capture, implantation of coded transmitter tags, and release of 54 snapper (Table 5.4). Fish were captured using handlines or longlines either in the vicinity of the array of receivers in NGSV or at several places in the northwest and southwest of the gulf (Fig. 5.3). Only snapper that were judged to be in reasonable condition and thought to have a good chance of survival were tagged using the following methodology. The captured fish was brought aboard the vessel and placed in a seawater tank that contained the anaesthetic AQUI-S at a concentration of 1.5 ml in a 50 L seawater bath (30 ppm) for 5–10 minutes. The subdued fish was then inverted in a cradle, whilst maintaining the anaesthesia by recirculating the AQUI-S solution across the fish's gills using a hose and small bilge pump. A towel was used to protect the fish's eyes and to reduce the stress associated with capture and handling. A small incision was made into the coelomic cavity anterior to the anus and the Vemco coded transmitter was inserted into the body cavity. The incision was stitched using external sutures. The fish was then measured, tagged externally, and injected with oxytetracycline at a dose of 0.2 $ml.kg^{-1}$ body weight into the dorsal musculature, to help prevent infection. It was then allowed to recover from the anaesthetic in a separate seawater tank for 10–60 minutes depending on its condition, before it was released.

The 54 tagged fish were from the broad size range of 32 to 97 cm caudal fork length (CFL). These included a number of 'small' (<40 cm CFL), numerous 'medium' (40-60 cm CFL), 'large' (60-80 cm CFL) and 'very large' fish (>80 cm CFL) (Fig. 5.4). Most small and medium fish were captured with rod and line and were tagged with V13 tags (Table 5.3). All fish >60 cm CFL were captured with longlines and were tagged either with V13P or V16 tags.

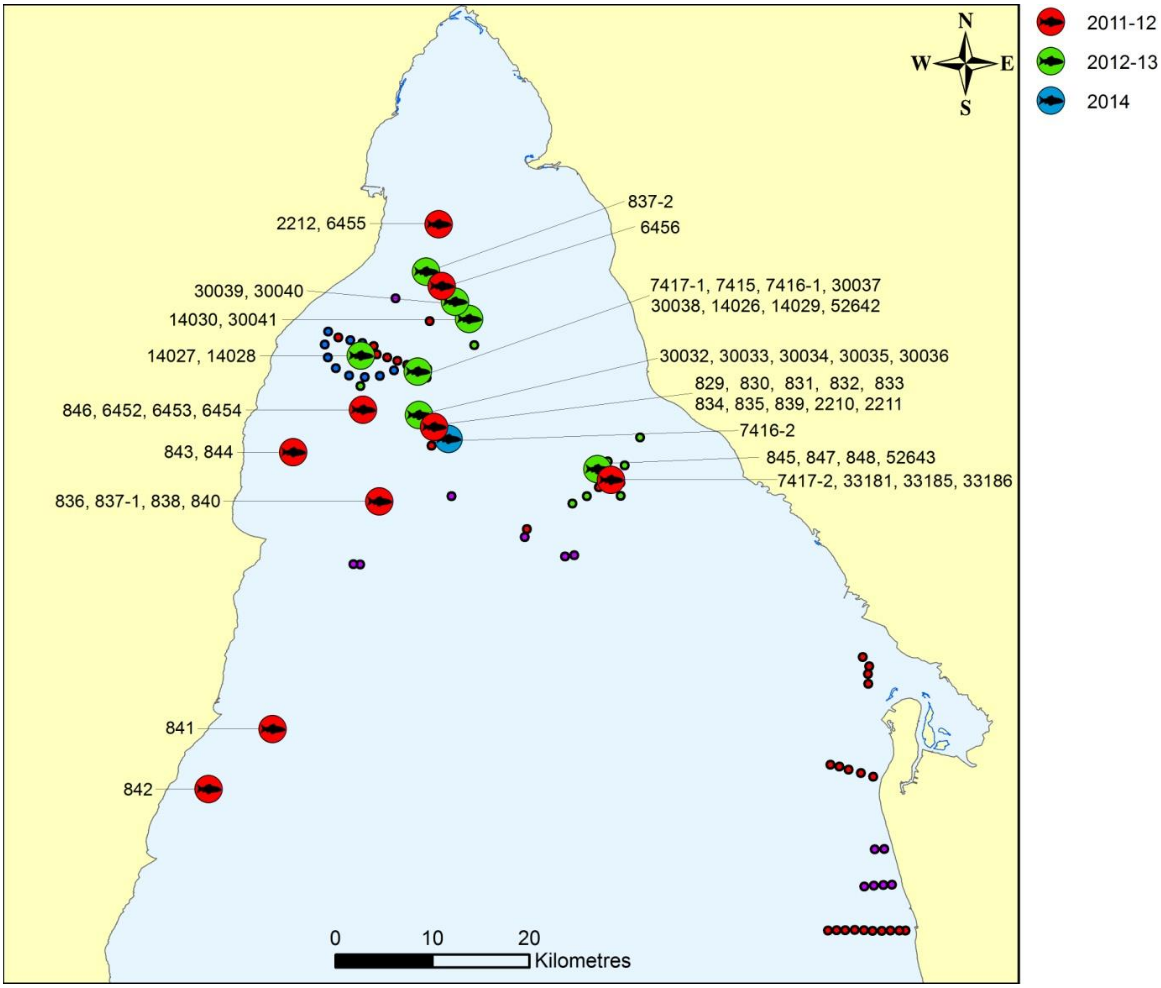


Fig. 5.3 Map of Gulf St. Vincent showing the places where snapper were captured, tagged with acoustic tags and then released. For details refer to Table 5.4. Numbers indicate the identification number of each fish. The locations of acoustic receivers are also shown.

Table 5.4 Details of successful tagging events in NGSV between May 2011 and May 2014, including when and where each tag was deployed, tag type, its estimated life as well as the gear used to capture the fish and the fish size. Tag sites relative to the locations of acoustic receivers are indicated on Fig. 5.3. (HL - handline, LL – longline).

Identification no.	Date tagged	Tag site	Fishing gear type	Fish size (CFL-cm)	Tag type	Estimated tag life (days)
829	26-May-11	Zanoni wreck	HL	54	V13-1L	623
830	26-May-11	Zanoni wreck	HL	40	V13-1L	623
831	26-May-11	Zanoni wreck	LL	46	V13-1L	623
832	26-May-11	Zanoni wreck	LL	39	V13-1L	623
833	26-May-11	Zanoni wreck	HL	36	V13-1L	623
834	26-May-11	Zanoni wreck	HL	45	V13-1L	623
835	26-May-11	Zanoni wreck	HL	56	V13-1L	623
839	27-May-11	Zanoni wreck	HL	56	V16-5H	484
840	30-May-11	Black Point	HL	52	V16-5H	484
836	30-May-11	Black Point	HL	51	V13-1L	623
837-1	30-May-11	Black Point	HL	50	V13-1L	623
838	21-Sep-11	Black Point	HL	47	V13-1L	623
841	21-Sep-11	Pt Vincent	LL	81	V16-5H	484
842	22-Sep-11	Stansbury Nth	LL	74	V16-5H	484
843	27-Sep-11	Rogues Point	LL	76	V16-5H	484
890	28-Sep-11	Rogues Point	LL	89	V16-5H	484
2210	28-Sep-11	Zanoni wreck	HL	53	V13-1L	623
2211	28-Sep-11	Zanoni wreck	HL	45	V13-1L	623
6452	05-Oct-11	Agros	LL	85	V13P-1L	399
6453	05-Oct-11	Agros	LL	88	V13P-1L	399
6454	06-Oct-11	Agros	LL	78	V13P-1L	399
846	06-Oct-11	Agros	LL	80	V16-5H	484
2212	06-Oct-11	Price	LL	68	V13-1L	623
6455	06-Oct-11	Price	LL	72	V13P-1L	399
6456	03-Nov-11	Macs Beach	HL	39	V13P-1L	399
845	24-Feb-12	Long spit (inner)	LL	80	V16-5H	484
847	24-Feb-12	Long spit (inner)	LL	83	V16-5H	484
848	24-Feb-12	Long spit (inner)	LL	82	V16-5H	484
52643	24-Feb-12	Long spit (inner)	LL	97	V16-5H	2116
30032	02-Oct-12	Zanoni wreck	HL	48	V13-1L	754
30033	02-Oct-12	Zanoni wreck	HL	54	V13-1L	754
30034	02 Oct 2012	Zanoni wreck	HL	42	V13-1L	754
30035	02 Oct 2012	Zanoni wreck	HL	46	V13-1L	754
30036	02 Oct 2012	Zanoni wreck	HL	45	V13-1L	754
14026	03 Oct 2012	Ardrossan	LL	75	V16P-4H	774
14027	03 Oct 2012	Ardrossan	LL	65	V16P-4H	774
14028	03 Oct 2012	Ardrossan	LL	72	V16P-4H	774
30037	03 Oct 2012	Ardrossan	LL	69	V16-4H	863
30038	03 Oct 2012	Ardrossan	LL	69	V16-4H	863
837-2	08 Oct 2012	Macs Beach	HL	48	V13-1L	320
14030	08 Oct 2012	Ardrossan	LL	82	V16P-4H	774
30041	08 Oct 2012	Ardrossan	LL	80	V16-4H	863
30039	09 Oct 2012	Ardrossan	LL	65	V16-4H	863
30040	09 Oct 2012	Ardrossan	LL	64	V16-4H	863
14029	09 Oct 2012	Ardrossan	LL	86	V16P-4H	774
7417-1	09 Oct 2012	Ardrossan	LL	80	V13P-1L	727
7415	09 Oct 2012	Ardrossan	LL	74	V13P-1L	727
7416-1	09 Oct 2012	Ardrossan	LL	90	V13P-1L	727
52642	09 Oct 2012	Ardrossan	LL	89	V16-6H	2,116
33181	11 Jan 2013	Long Spit (inner)	LL	81	V16-6H	2,116
7417-2	11 Jan 2013	Long Spit (inner)	LL	69	V16P-4H	680
33185	11 Jan 2013	Long Spit (inner)	LL	70	V16-6H	2,116
33186	11 Jan 2013	Long Spit (inner)	LL	86	V16-6H	2,116
7416-2	23 May 2014	Zanoni wreck	HL	32	V13P-1L	544

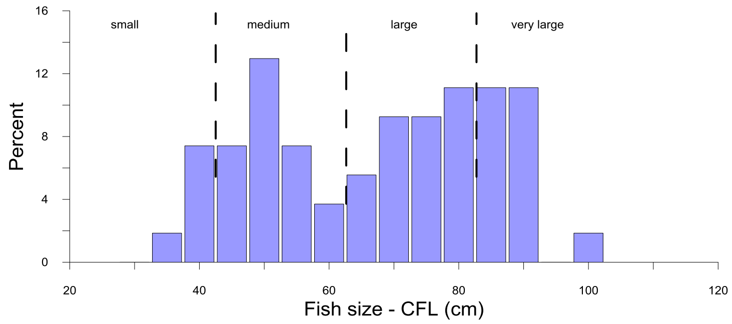


Fig. 5.4 Length frequency distribution for the snapper tagged with acoustic tags in Northern Gulf St. Vincent. Also, shown are the boundaries of the size categories used in the text for snapper. CFL – caudal fork length.

5.2.4 Data retrieval and analysis

The acoustic receivers were retrieved 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 2014, although due to poor weather several receivers were not finally retrieved until the 22 July 2014. The retrievals were done by scuba divers.

Data recorded by the acoustic receivers were downloaded using the software package VUE Version 1.08.001 (Vemco Ltd, Nova Scotia, Canada). Later, all downloaded files from the three-year study were compiled into a single database. Data were exported to Excel for exploration and analysis and included the data fields of: date and time in Coordinated Universal Time; tag identification number; receiver number; and station identification code. Data on water depth were not considered here. For all data processing, the date/time field was converted to Australian Central Standard Time.

Space use – timing and duration of occupancy of study area

Pivot tables were used to generate annual totals of detections that were subsequently considered at several spatial scales, i.e. amongst areas and amongst the different stations. Similarly, the numbers of tagged snapper that contributed to the detections were determined to calculate the numbers of detections per tagged fish per receiver.

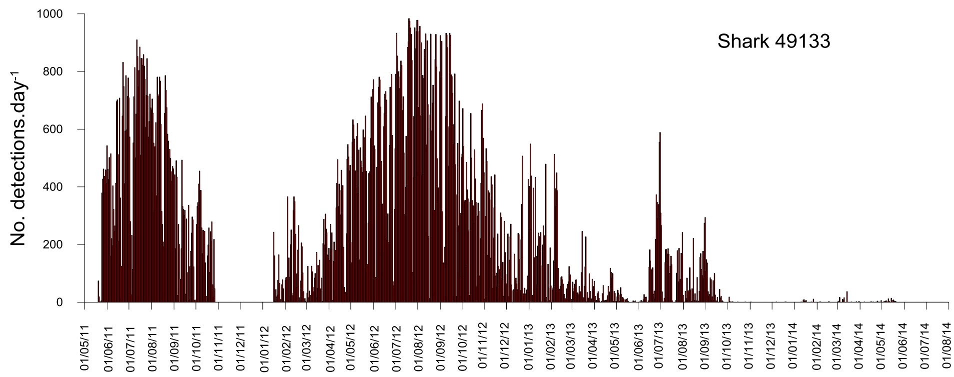
With respect to temporal analysis, several measures of the use of the study area by each tagged fish were calculated. The ‘detection period’ was the number of days between the date of capture/tagging and the date of last detection. The ‘residence index’ (RI) was calculated by dividing the total number of days that the snapper was recorded across all stations by the period of viability of its tag, or up until the last data download, whichever came first. This overall RI was divided into the proportions of time recorded in each of the six component areas of the study area.

Consideration of the detection data to describe the temporal use of the study area was more complex, based on findings of an earlier acoustic telemetry study done in NGSV for whaler sharks (*Carcharinus brachyurus* and *C. obscurus*) (Huveneers et al. 2012). That study demonstrated a significant environmental influence on the acuity of the system to record detections. For a long-term 'sentinel' tag from a tagged shark that died in the vicinity of an acoustic receiver, more detections were recorded in winter than summer, presumably reflecting the influence of background noise on the capability of the receiver to detect the pings from the tag. This complexity indicated that any long-term temporal study in NGSV would need to take such seasonal variation in acuity into consideration. To achieve this in our study, data from two long-term 'sentinel' tags were considered, i.e. the shark from the earlier study as well as one of our tagged snapper. Shark 49133, a bronze whaler (*C. brachyurus*) had died near 24LS on the 20th May 2011, and its acoustic tag continued to transmit until early 2014, although the declining detection rate through 2013 suggested that the battery became weaker through 2013 (Fig. 5.5). The tagged snapper (Fish 52642) died in the vicinity of 17ZN on the 15th March 2013 where it was detected until 22 July 2014, producing a total of 198,735 spurious detections. The daily detection data from Tags 49133 and 52642 demonstrated considerable seasonal variation (Fig. 5.5). From the two datasets, a single time-series was developed that included the records from Tag 49133 from 20th August 2011 to 14th March 2013 and from Tag 52642 from 15 March 2013 to 22 July 2014. From this time-series, the numbers of detections were calculated for every month from June 2011 to June 2014. Then the mean and standard deviations for numbers of detections per calendar month were estimated across years. Finally, the standardised monthly detection frequencies were calculated using the equation of Payne et al. (2010):

$$SDF_b = B_b / \mu$$

where μ is the mean detection frequency across the 12 monthly bins (b) and B is the mean detection frequency for each of the 12 monthly bins.

To develop the time series of detections of snapper in the study area, the numbers of detections for each month for the viable fish were calculated from the raw data. These values were then standardised to the acuity of the system by dividing by the calculated SDFs. Similarly, the standardised detection rates were calculated for each area of AN, AR, AG, ZN and LS.



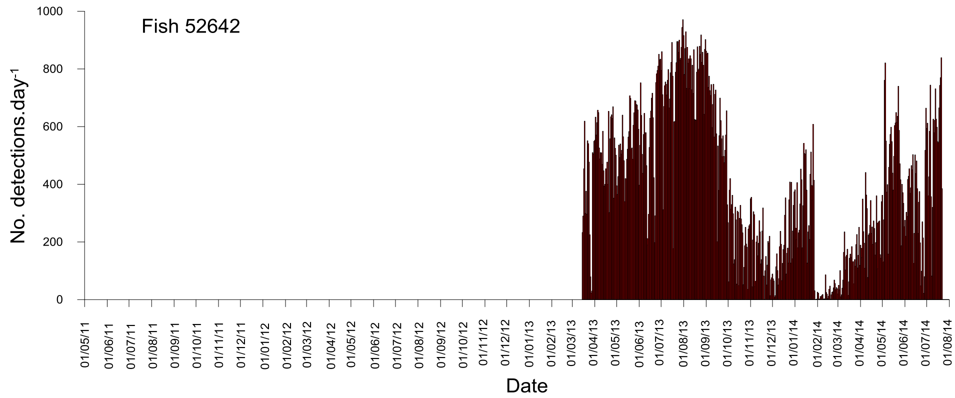


Fig. 5.5 Frequency distributions for detections of two ‘sentinel’ tags that resulted from the deaths of Shark 49133 and Fish 52642.

Patterns of movement

The behaviour of each tagged snapper was considered by generating a figure that showed the days on which the fish was detected at the different stations. Such figures clearly demonstrate the temporal aspects of the movement behaviour in terms of duration of occupancy at particular stations and across stations in the same area, as well as the timing of movements between stations. For some fish, estimates of the distances moved at various times through their detection periods were calculated using ArcGIS, based on distances between consecutive stations where the fish was recorded. Also, for these fish, ArcGIS was used to generate a map that showed the track of successive detections between stations.

5.3 Results

Across the approximate three-year period of this project, a total of 720,302 detections were recorded from the 54 tagged snapper. These included the 198,735 spurious detections after the death of Fish 52642 near Station 17ZN on 14 March 2013. Disregarding the latter, there was a total of 521,567 legitimate detections for interpretation in terms of fish behaviour. Of these, 521,544 detections were recorded in the study area in NGSV, whilst the remaining 23 were recorded in October 2012 and January 2013 from a single tagged fish along the Glenelg line of receivers (Fig. 5.2).

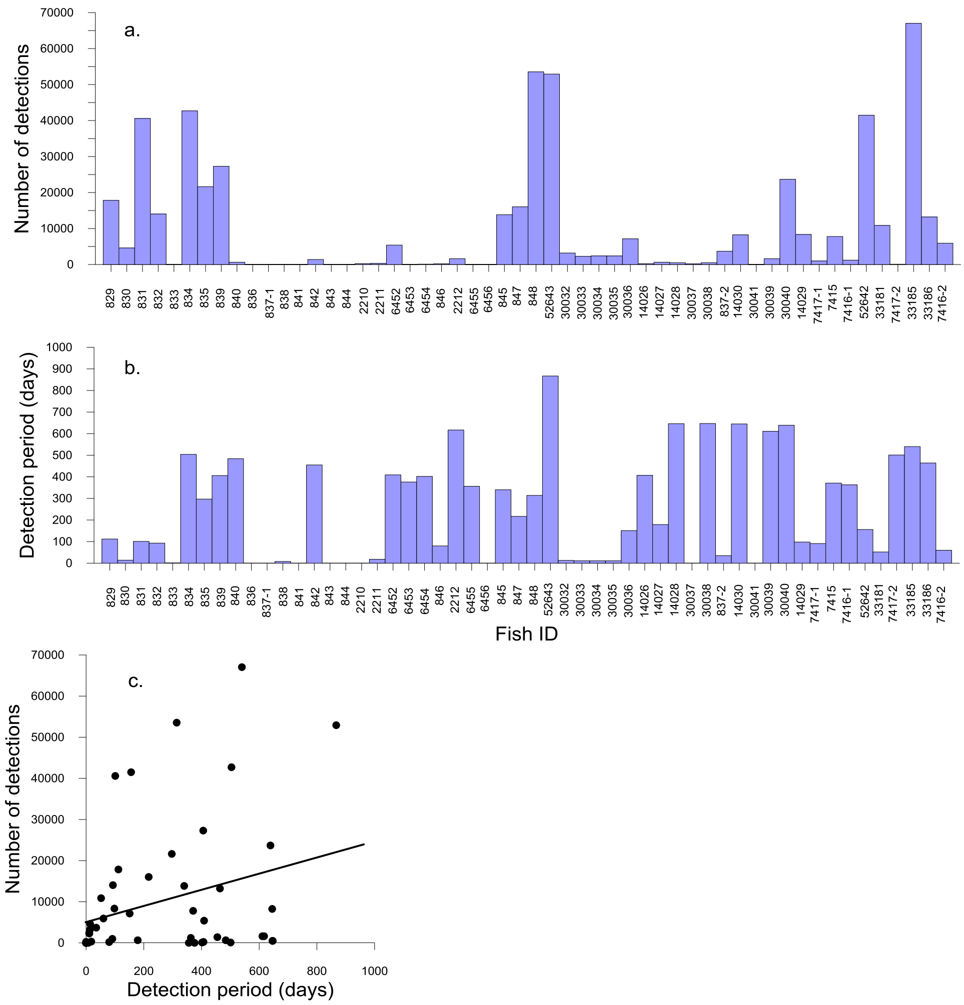


Fig. 5.6 Summary of results from the acoustic telemetry study in NGSV. a. number of detections recorded for each tagged fish in the order in which they were tagged; b. detection period in days for each fish; c. relationship between number of detections and detection period, showing the significant linear relationship.

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Table 5.5 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						

The total number of detections per individual varied considerably, ranging from zero to 67,040 (Table 5.5, Fig. 5.6a). Seven fish produced no detections and for a further 14 fish there were <500 detections. In contrast, 15 fish produced >10,000 detections each. The detection periods were also highly variable and ranged from zero to 867 days (Table 5.5, Fig. 5.6b). For 31 fish, the detection period exceeded 100 days, and for 19 of these it exceeded one year. There was a significant linear relationship between the number of detections and the detection period, although the relationship was weak and accounted for only 8% of the variation in numbers of detections (No. of detections = 20.92*(Detection period) + 4,349.2, $n = 54$, $p = 0.02$*, $r^2 = 0.08$) (Fig. 5.6c)

5.3.1 Space use – timing and duration of occupancy of study area

The BP area was difficult to work because of water depth, whilst of the two detectors deployed there in 2011, one was lost and the other produced no detections. As such, this area was not considered after April 2012. For the other five areas, detections of snapper were recorded in each of the three years, although with an uneven contribution from each (Fig. 5.7a). 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% of detections accounted for by decreasing contributions from AR, AG and AN, respectively. The uneven spatial contribution of detections was consistent amongst years (Fig. 5.7a). It related partly to differences in the numbers of snapper detected per area, with the numbers marginally higher at ZN compared to several of the other areas (Fig. 5.7b). However, the uneven spatial contribution 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. 5.7c), indicating that, on average, individual fish spent considerably longer durations in the ZN area than the other areas.

When considered at the scale of station, 17ZN consistently accounted for the highest number of detections in each of the three years (Fig. 5.8a,b,c). This station was visited by the highest number of tagged fish (Fig. 5.8d,e,f), and the average rate of detections was generally several orders of magnitude higher than for other stations (Fig. 5.8g). 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.

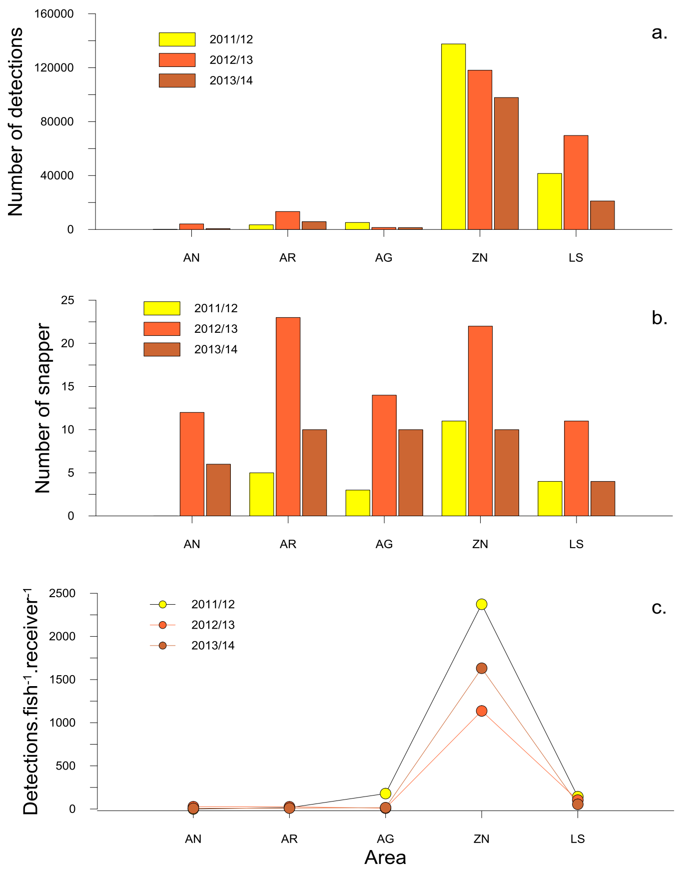


Fig. 5.7 Summary of spatial results of the acoustic telemetry study in NGSV at the scale of area. a. number of detections recorded per year in the five areas where detections were recorded; b. number of snapper detected per year in each area; c. number of detections per viable fish per acoustic receiver in each area. For locations of areas refer to Fig. 5.2.

The estimates of RI were highly variable (Fig. 5.9a). For most fish the estimated RI was relatively low at <0.1, however, there were 15 fish for which the RI was >0.1, including eight fish for which it ranged from 0.2 to 0.6. There was no significant relationship between RI and CFL (n = 54, p = 0.271, r^2 = 0.0044) (Fig. 5.9b).

Temporal analysis

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 and that different fish were detected at different times and for different durations (Fig. 5.10). As such, fish used the study area in different ways.

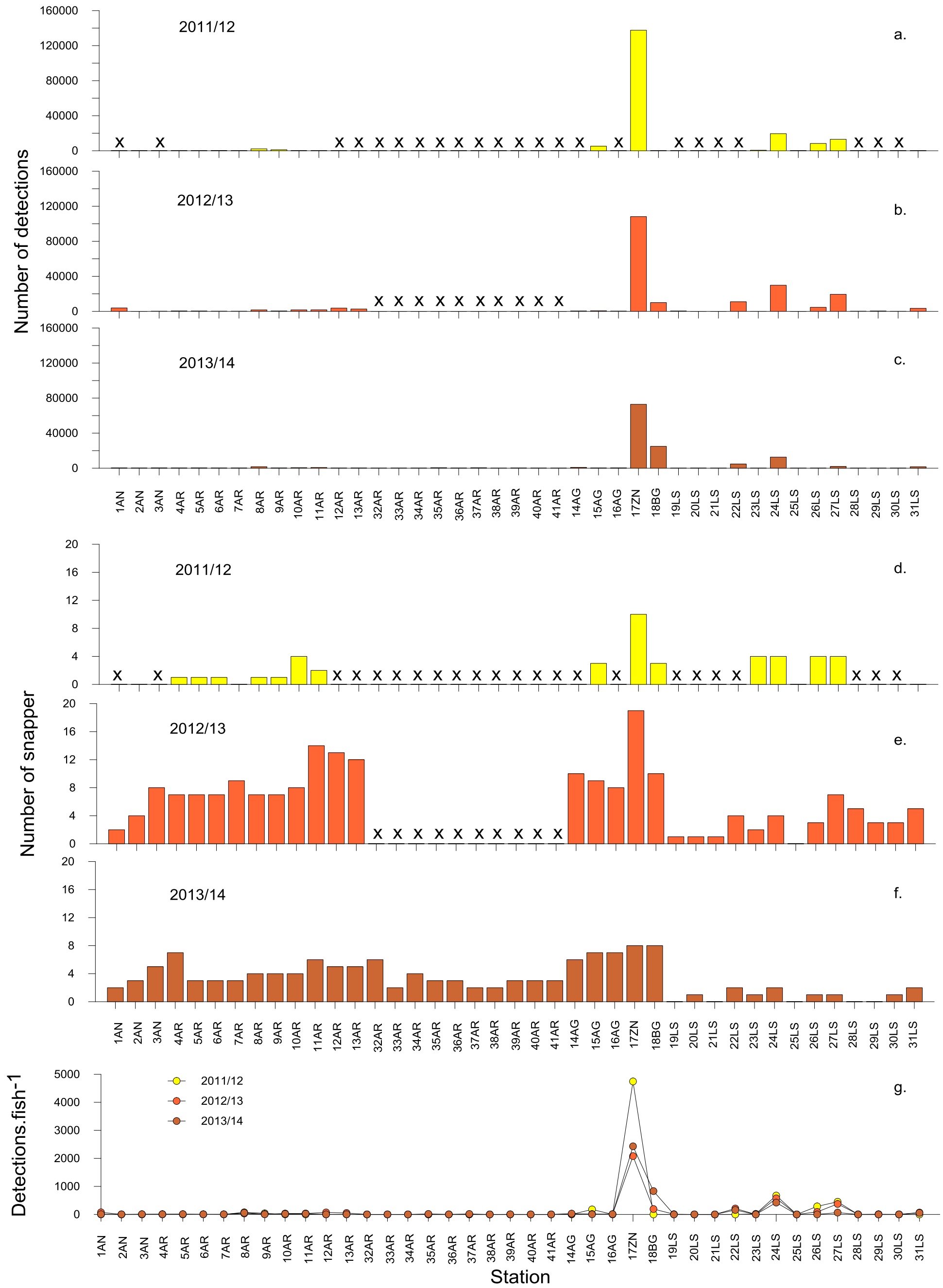


Fig. 5.8 Summary of spatial results of the acoustic telemetry study in NGSV at the scale of station. a, b, c. detections recorded per year at each station; d, e, f. number of snapper detected per year at each station; g. number of detections per viable fish per station. 'x' indicates that station was not monitored in that year.

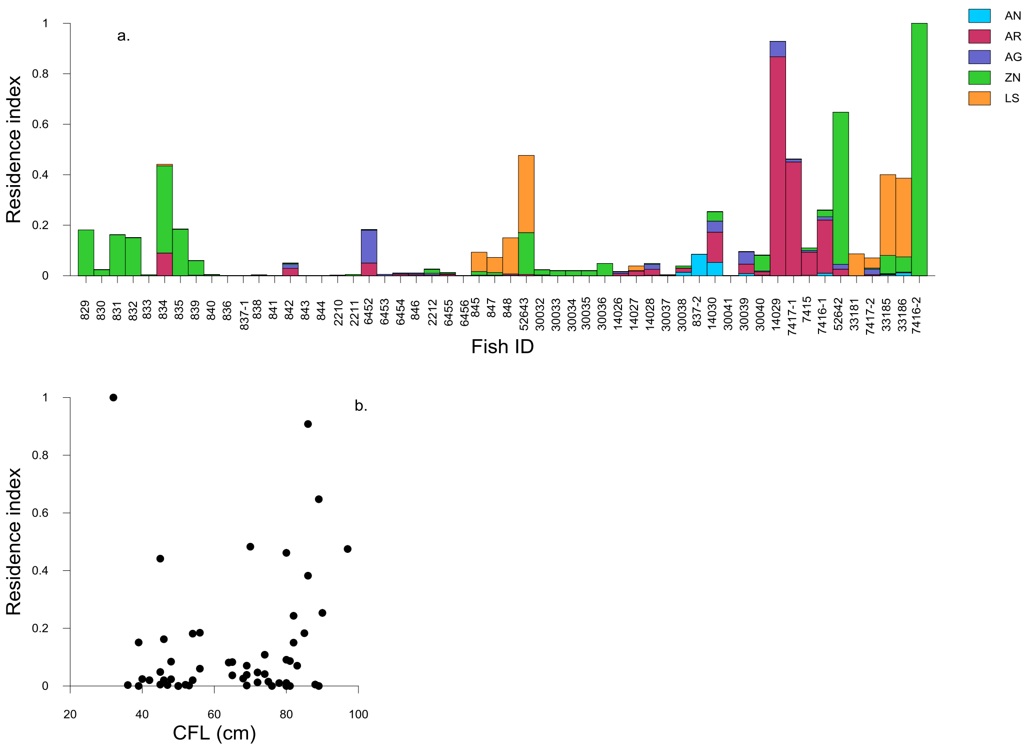


Fig. 5.9 Summary of spatial results of the acoustic telemetry study in NGSV. a. estimates of Residence Index for the whole study area divided into proportions of time spent in the different component areas; b. relationship between Residence Index and fish size.

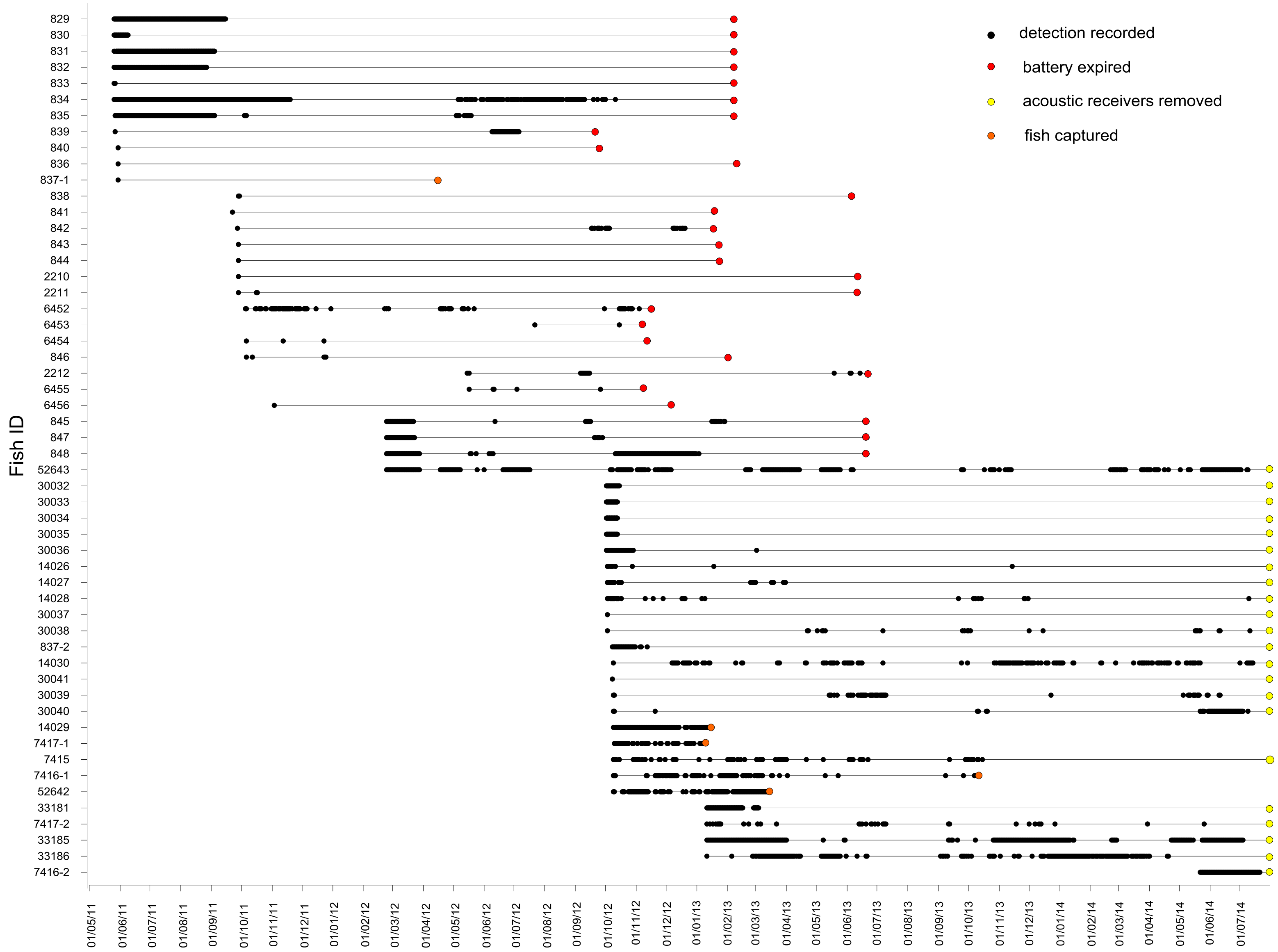


Fig. 5.10 Timing of the detections of the tagged fish in the acoustic telemetry study from when first tagged to either when the battery expired, the fish was captured or the study was terminated.

The total number of stations where fish were detected was highly variable over time (Fig. 5.11). This probably reflects the influence of numerous factors including number of viable fish, as well as when and where they were tagged. Nevertheless, there were two periods when tagged snapper were recorded at numerous stations, (i.e. through the spring/summer of 2012/13 and the spring of 2013), suggesting that the fish were more active and mobile during these seasons.

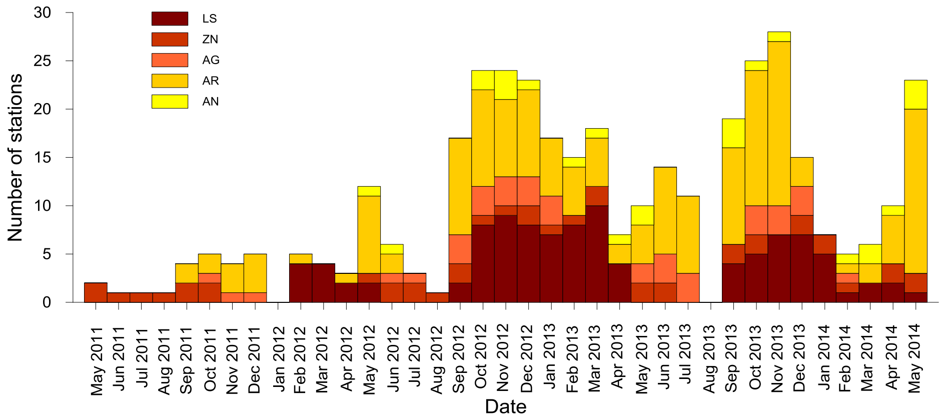


Fig. 5.11 Total number of stations in the study area in NGSV at which tagged snapper were detected per month across the three year study period.

The numbers of detections across all tagged individuals for the whole study area and each of the five component areas were standardised according to the monthly SDFs. The standardised detection rate for fish across the whole study area was highly variable amongst months, but with several modes evident in the time series, i.e. in the winters of 2011 and 2014, and each summer of 2011/12, 2012/13 and 2013/14 (Fig. 5.12a). The modes in detection rates for the whole study area 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. 5.12b,c,d,f). In contrast, it was the high rate of detections in the ZN area that was responsible for winter peaks in both 2011 and 2014 (Fig. 5.12e). These data indicate that the dispersion of the fish changed seasonally. They were more broadly dispersed and detected at a higher number of stations in summer, which again suggests that the fish were more active and mobile at this time of the year.

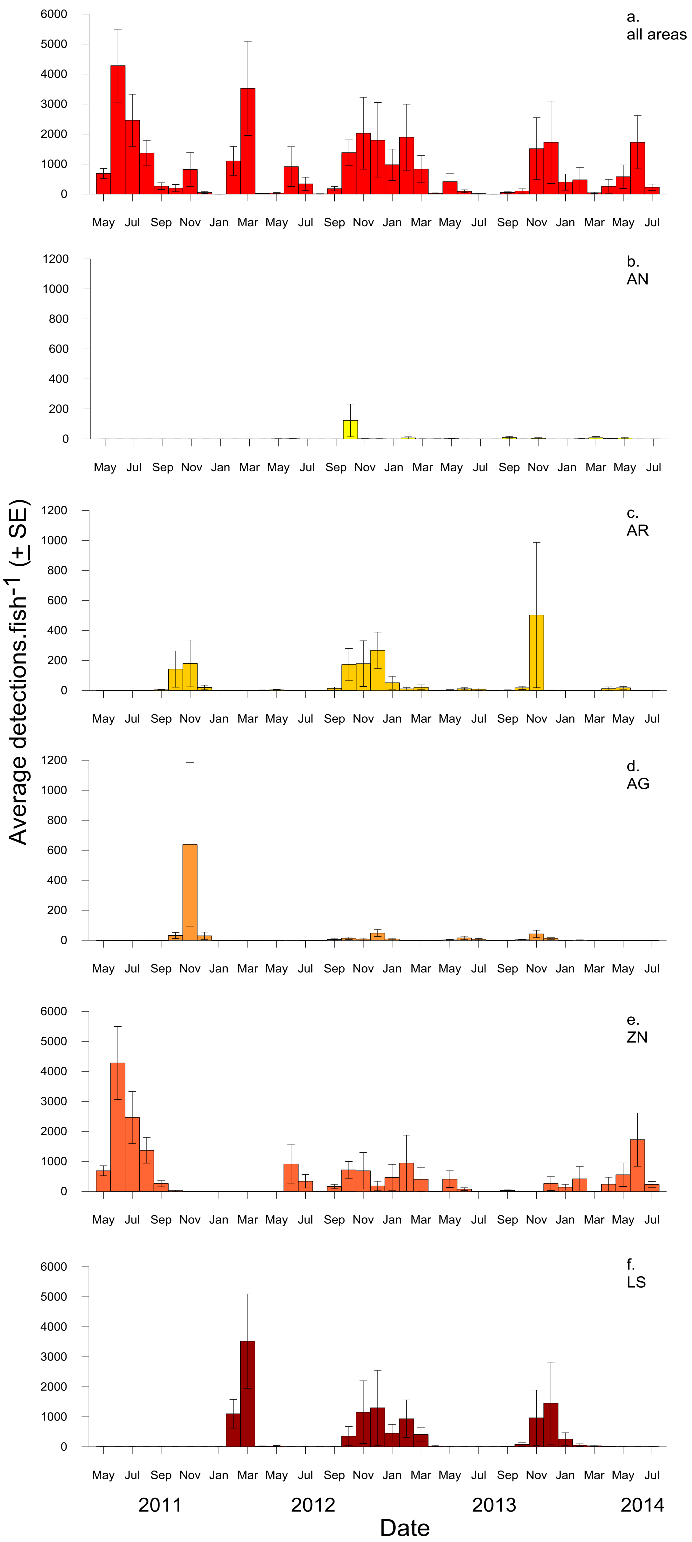


Fig. 5.12. Summary of spatial and temporal results from the acoustic telemetry study in NGSV. a. estimates of monthly detection rates across the whole study area for the duration of the study from May 2011 until July 2014. b, c, d, e, f show the monthly detection rates per viable fish for each of the five component areas for the duration of the study. Note the different scales on the Y-axes for different areas. For locations of areas refer to Fig. 5.2.

5.3.2 Fish behaviour

For 10 fish, either no detections or only a small number were recorded up to a day or two subsequent to tagging. These were Fish nos. 833, 836, 837-1, 841, 843, 844, 2210, 6456, 30037 and 30041 (Table 5.5). Those that produced no detections were generally captured, tagged and released some considerable distance from the study area, and therefore distant from any listening station. The fate of most of these 10 fish subsequent to tagging is unknown, and may have ranged from simply remaining outside the study area to being caught in a fishing operation. Only the fate of Fish 837-1 is known, i.e., after being captured and tagged at BP on 30 May 2011 it was recaptured 10.5 months later, by a recreational fisherman near where it had been tagged.

Each of the remaining 44 fish was detected a sufficient period after tagging to know that it had survived the tagging process (Fig. 5.10). The numbers of detections and patterns over time varied considerably amongst fish, reflecting different ways the study area was used.

Temporary residents

One behavioural category for snapper evident in this study was the 'temporary residents', i.e. fish that were detected at the same station every day for periods of weeks to months. The category included Fish 829, 831, 832, 834 and 835 that were amongst the first tagged in the study (Fig. 5.10), which occurred near station 17ZN on 26 May 2011. Each of these fish was subsequently recorded at 17ZN every day for several months until at least 27 August 2011 (Fig. 5.10). Because of this relatively sedentary behaviour through winter, high numbers of detections were recorded. From May to September 2011, these five fish contributed a total of 132,110 detections, which represented 25.3% of the total number of detections recorded in the study. Throughout their detection periods until at least late August 2011, the standardised daily detection rate varied over several temporal scales (Fig. 5.13). The highest detection rates were between late May and mid-late July. They declined through August and September, indicating that the fish spent less time each day in the vicinity of 17ZN before eventually moving away by late September. Fish 829, 830 and 831 were never subsequently recorded, and so their fates are unknown. Fish 835 returned briefly to 17ZN first on the 5-6 Oct 2011 and then again from the 4^{th}-19^{th} May 2012. More data were available for Fish 834. After months of sedentary behaviour at Station 17ZN during winter 2011, it departed on the 25 September and within 12 hours was located at 8AR, i.e. 7.4 km away, where it remained for several months (Fig. 5.14). During 2012, the seasonal behavioural sequence was essentially repeated as it again resided at 17ZN for several months during winter before departing and heading north to 8AR during spring.

Fishes 30032, 30033, 30034, 30035 and 30036 were also in this category of 'temporary residents' (Fig. 5.10). They were all tagged on 2 October 2012 at 17ZN, where each was subsequently detected daily for up to 27 days. In total, they accounted for 17,395 detections through this period, (i.e. 3.3% of the total recorded in the study area). Of these five fish, Fishes 30033, 30034 and 30035 were never recorded subsequently and so their fate is unknown. Fish 30036 was recorded back at 17ZN in early March 2013. Fish 30032 headed north from 17ZN in spring and travelled 5.1 km to 12AR in less than three hours before moving another 8.7 km to 1AN (Fig. A11.1).

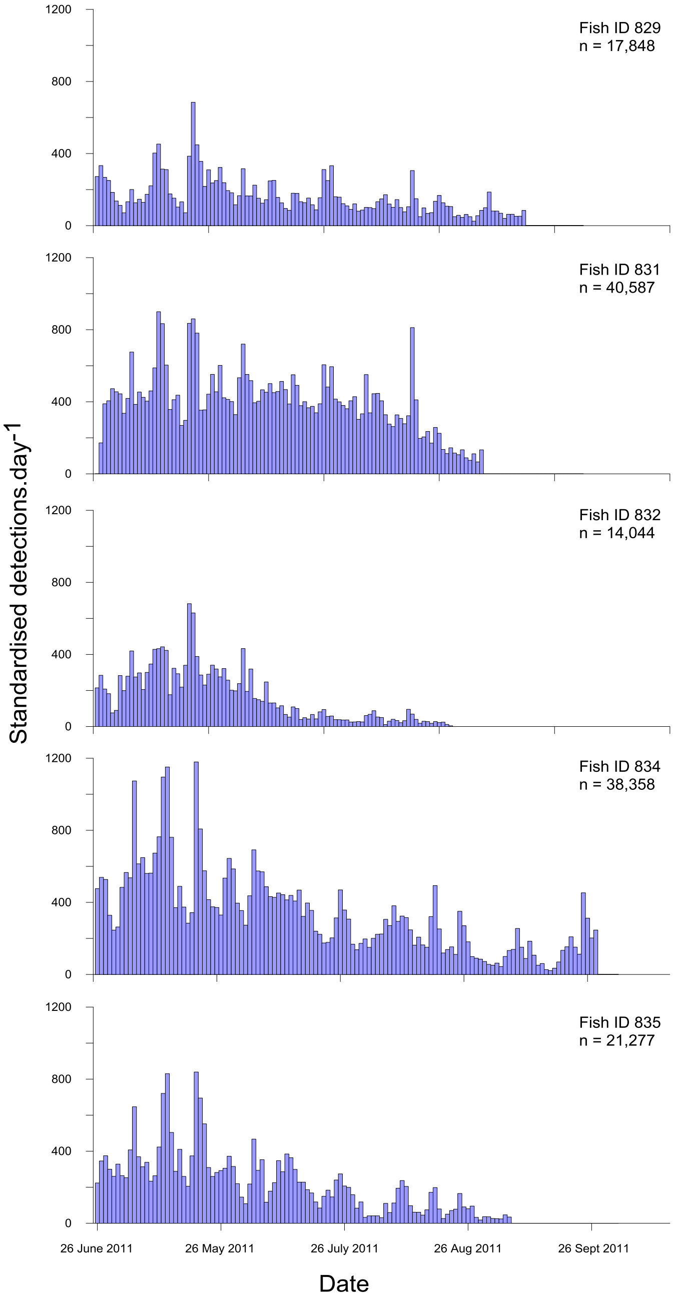
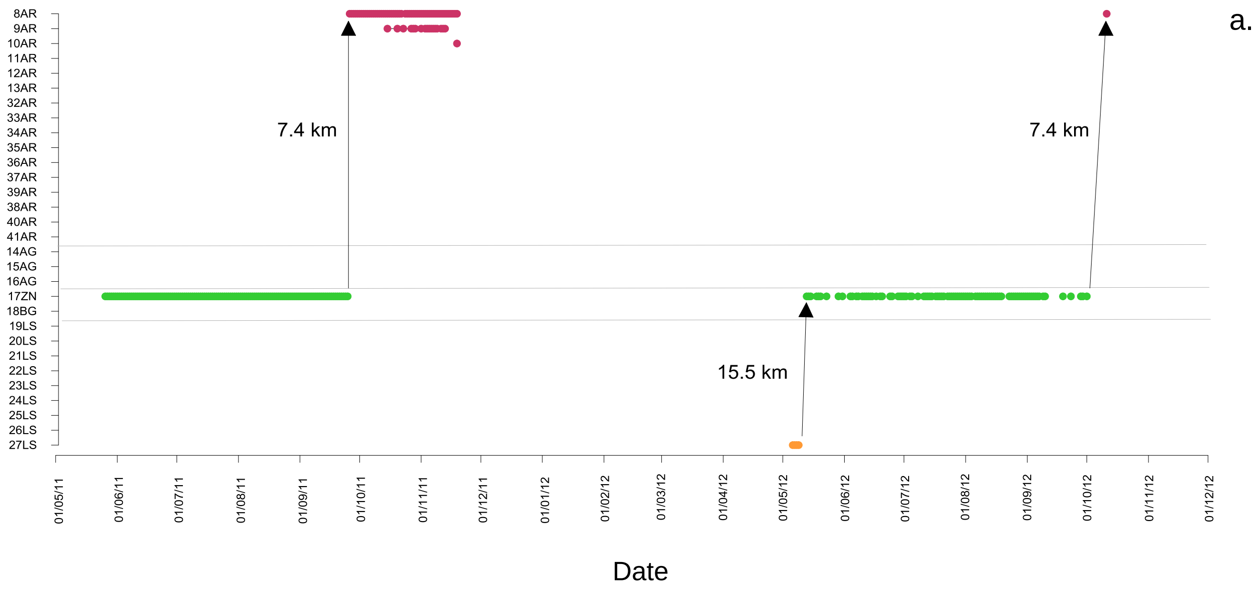


Fig. 5.13 Summary of daily rates of detections at 17ZN for Fish 829, 831, 832, 834 and 835 from when first tagged in May 2011 until 1st November 2011.



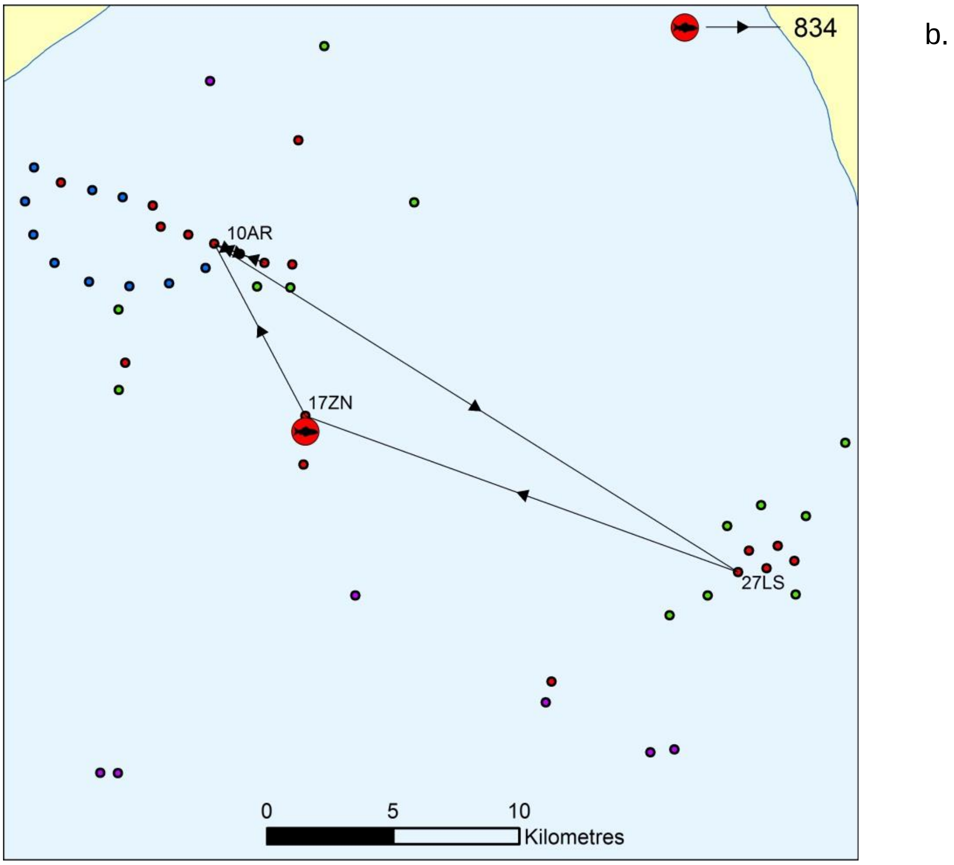


Fig. 5.14. Details of the movement behaviour of Fish 834 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

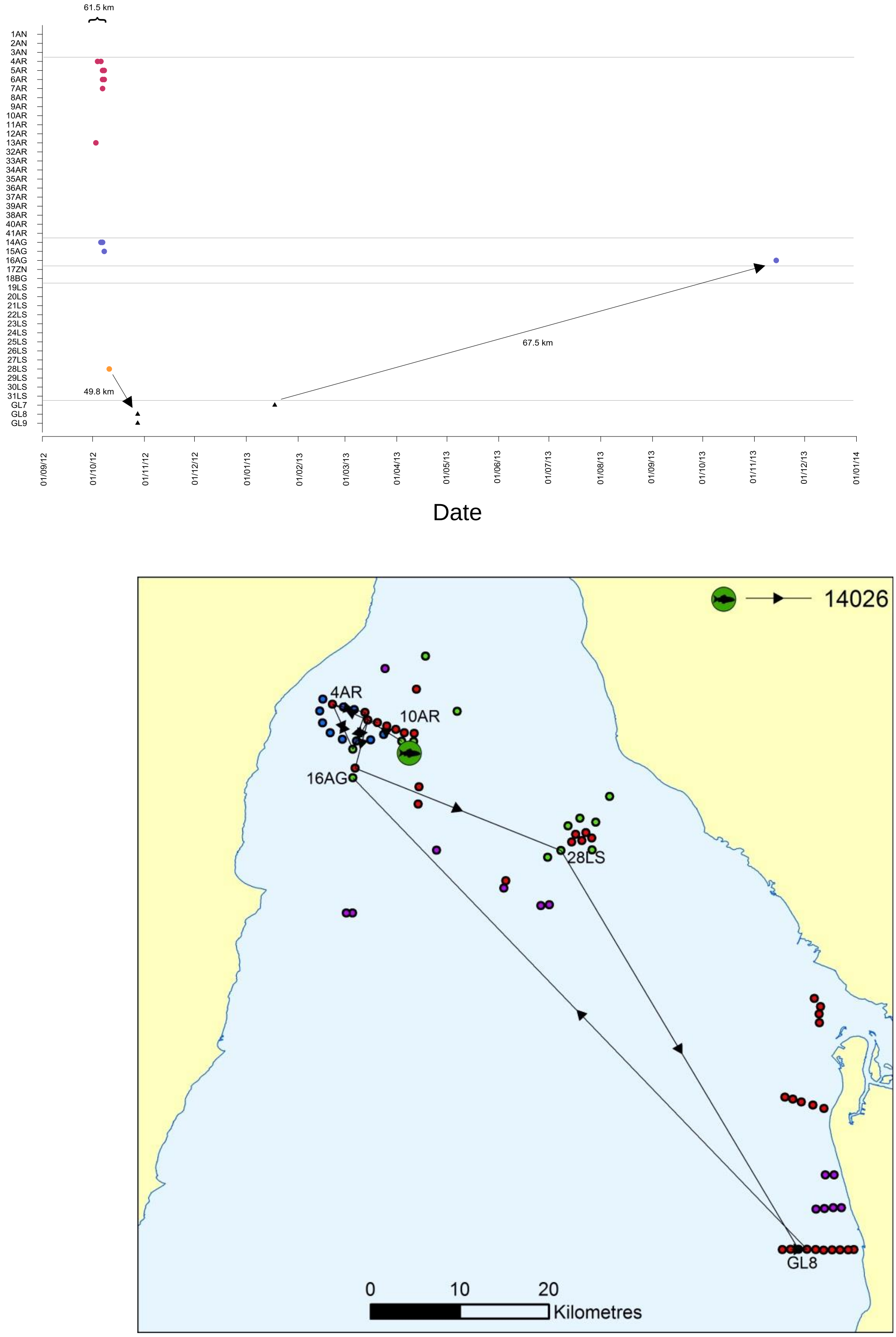
Transient, infrequent visitors

A number of fish were only detected occasionally in the study area and with few detections. They are categorised as 'transient, infrequent visitors' and included Fish 840, 6453, 6454, 6455, 2212, 14026, 14027, 14028, 33038 and 7417-2 (Fig. 5.10). They characteristically had relatively long detection periods, but low residence indices that were generally in the range of <0.01 to 0.04 (Table 5.5).

The detections of some of the transient, infrequent visitors were spasmodic. For example, Fish 840 was only recorded during a two-day visit to 17ZN in September 2012, 484 days after being tagged at BP on 30 May 2011. Similarly, after Fish 6454 was tagged in the AG area in October 2011, only a few detections were recorded in each of the AG and AR areas during November and December 2011, and then again in December 2012. After Fish 14026 was tagged on 3rd October 2012, it moved several times between the AR and AG areas and eventually to 28LS on 11th October, a distance between stations of 61.5 km (Fig. 5.15). From there, the fish was detected at the Glenelg receivers 49.8 km away on the 28 October. By November 2013 it had returned to NGSV. The total distance between stations was 182.5 km representing the longest north-south round trip recorded in the study.

Although Fish 14028 only spent minimal time in the study area in NGSV, there was considerable regularity in its visits and consistency in the places visited at different times of the year (Fig. 5.16). During the spring and summer of 2012/13, it moved back and forth several times between stations in the AR, AG and AN areas, over a distance of 57.7 km. In the following spring and summer, the fish visited the same or nearby stations, and covered a distance of 62.2 km. Other fish that demonstrated this type of behaviour are Fish 30038 and 7417-2 (Figs. A11.2, A11.3).

a.



b.

Fig. 5.15. Details of the movement behaviour of Fish 14026 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

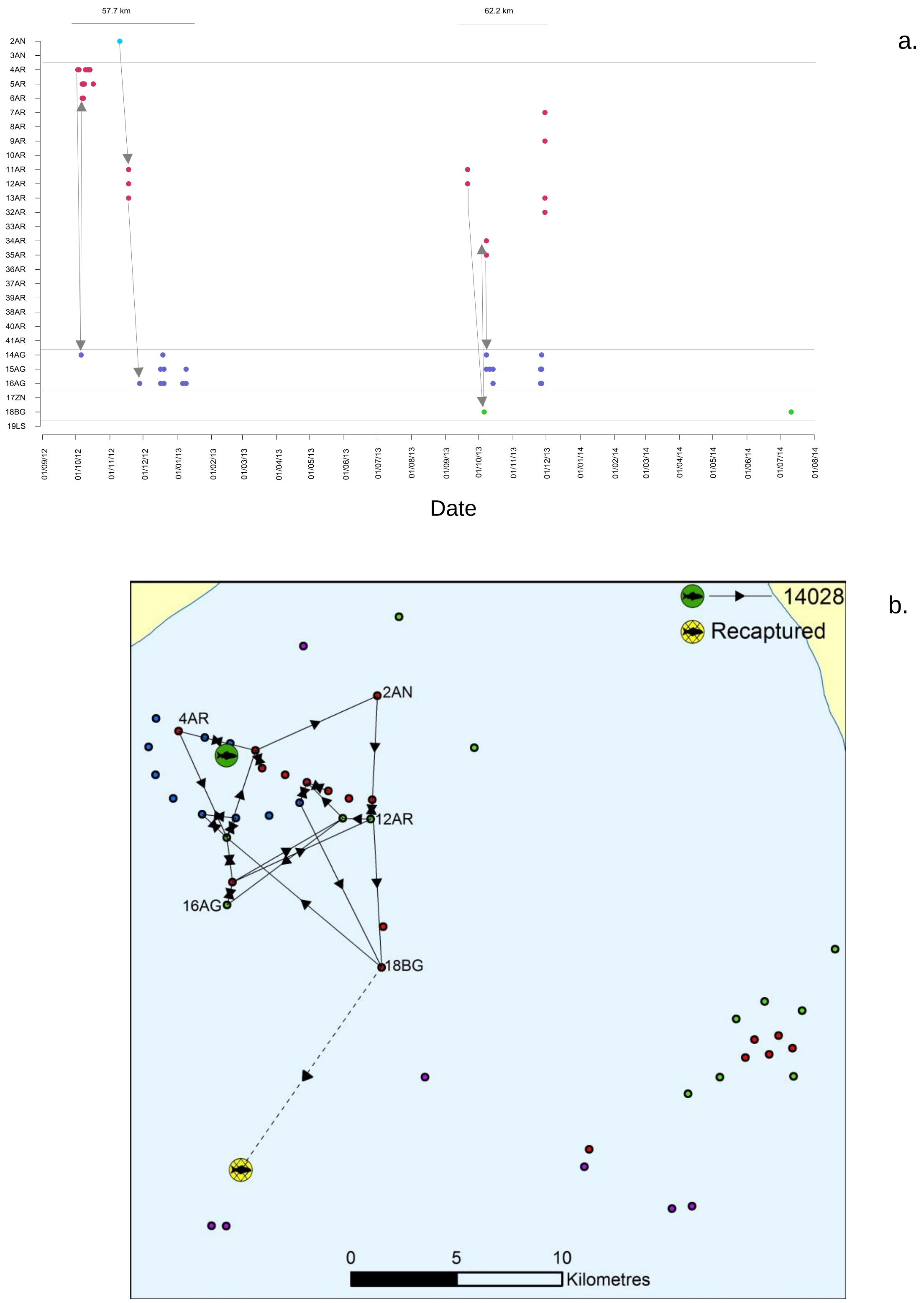


Fig. 5.16. Details of the movement behaviour of Fish 14028 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

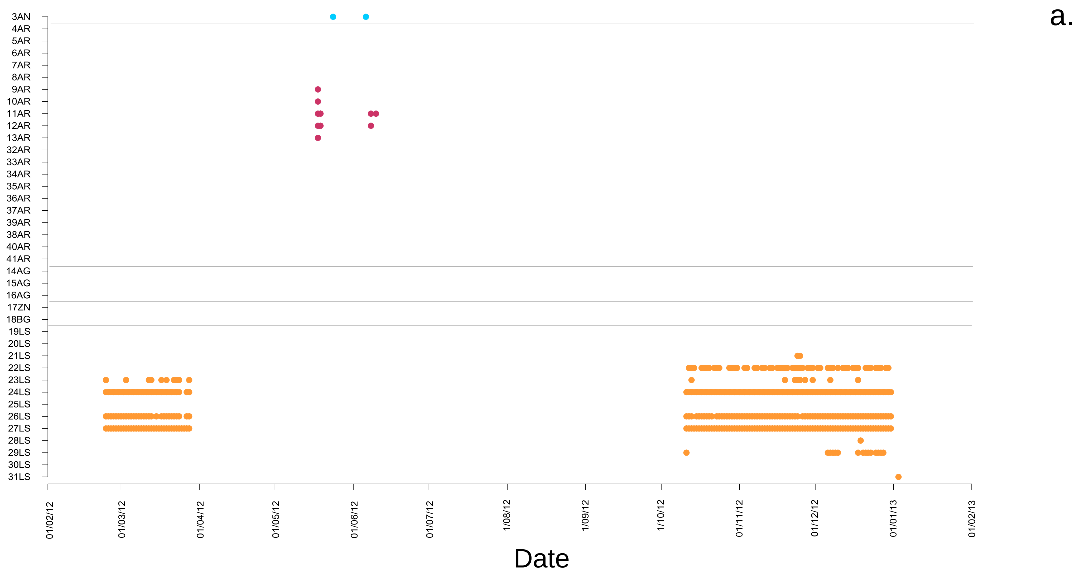
Mobile, partial residents

The third category of behaviour involved those fish that were detected in the study area on numerous occasions and for considerable durations throughout their detection periods. They spent more time in the study area than did the 'transient, infrequent visitors', whilst they were more mobile than the 'temporary residents'. They included Fish 6452, 848, 52643, 14030, 30039, 14029, 7415, 7416-1, 52642, 33185 and 33186 (Table 5.5, Fig. 5.10). They generally had RIs that exceeded 0.2 and were recorded in four of the five areas of the study area. However, at different times of the year their activity was concentrated around particular stations. Such fish are categorised as 'mobile, partial residents'.

Fish 848 was recorded in the LS area every day for durations of several months during late summer 2011/12 and in the early to mid-summer 2012/13 (Fig. 5.17). During these periods it consistently moved amongst a number of the LS stations, although most detections were recorded at 24LS, 26LS and 27LS. This area attracted 99.7% of its 53,545 detections, whilst the remaining 0.3% were recorded in the AN and AR areas. After leaving 24LS on 28 March 2013, this fish was next detected 20.4 km away at 9AR on 18 May 2013, and then moved a further 5.3 km to 3AN by 24 May.

Fish 52643 also spent considerable periods of summer in the LS area. However, these periods were punctuated by abrupt excursions to the AR area (Fig. 5.18). In late September 2013, it moved from 31LS to 12AR, 11AR, 8AR, 32AR and then to 17ZN, i.e. a total distance of 28.2 km in 20 hours. In comparison, during parts of three consecutive winters it was detected daily in the vicinity of 17ZN and 18BG. Fish 33185 and Fish 33186 also spent considerable periods of winter at 17ZN and 18BG, and their summers primarily in the LS area (Figs. A11.4, A11.5).

Not all of the 'mobile, partial residents' concentrated their activities around the ZN or LS areas. The detections for Fish 14030 were concentrated in the AR area in summer and autumn in two consecutive years (Fig. 5.19). However, its movement behaviour was complex as it made numerous excursions to the AN, AG and ZN areas. For example, from 24 November to 31 December 2013, the sequence of stations where this fish was recorded was; 11AR,10AR,13AR,15AG, 16AG, 12AR, 13AR, 10AR, 13AR, 18BG,17ZN,18BG, 17ZN, 18BG, 16AG, 15AG, 18BG,17ZN, 18BG, 12AR, 18BG. The sequence of movements added up to 18.9 km. In comparison, whilst the detections of Fish 14029, 7415 and 7416-1 were also concentrated in the AR area, their behaviour was not as complex as that demonstrated by Fish 14030. Most of their detections were recorded in the AG area, with only few detections recorded in the AR and ZN areas (Fig. A11.7, A11.8, A11.9).



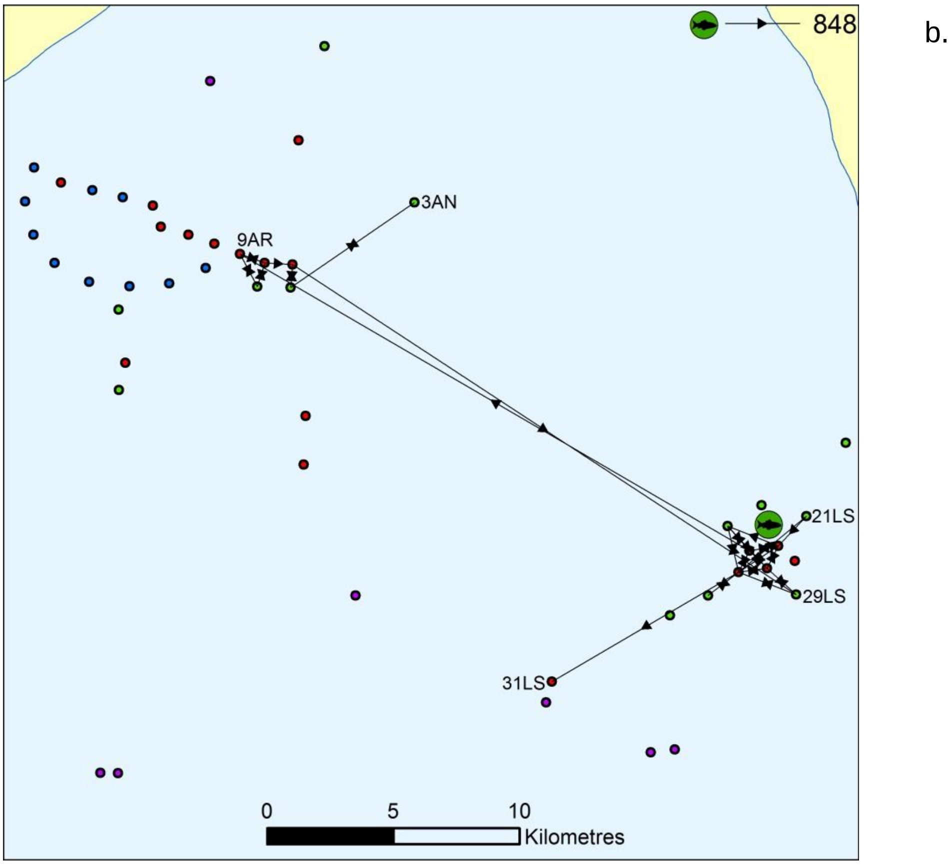


Fig. 5.17. Details of the movement behaviour of Fish 848 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

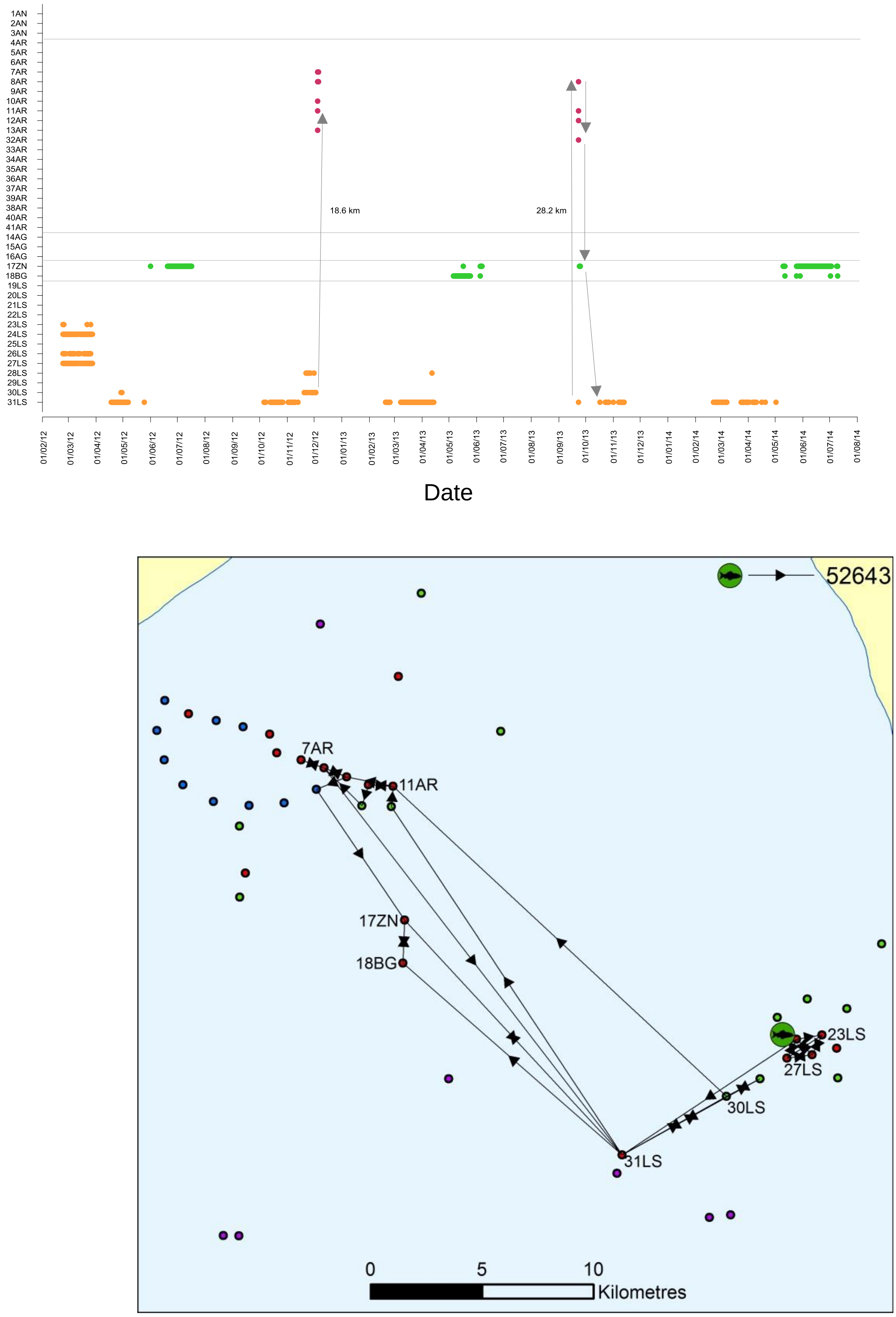


Fig. 5.18. Details of the movement behaviour of Fish 52643 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

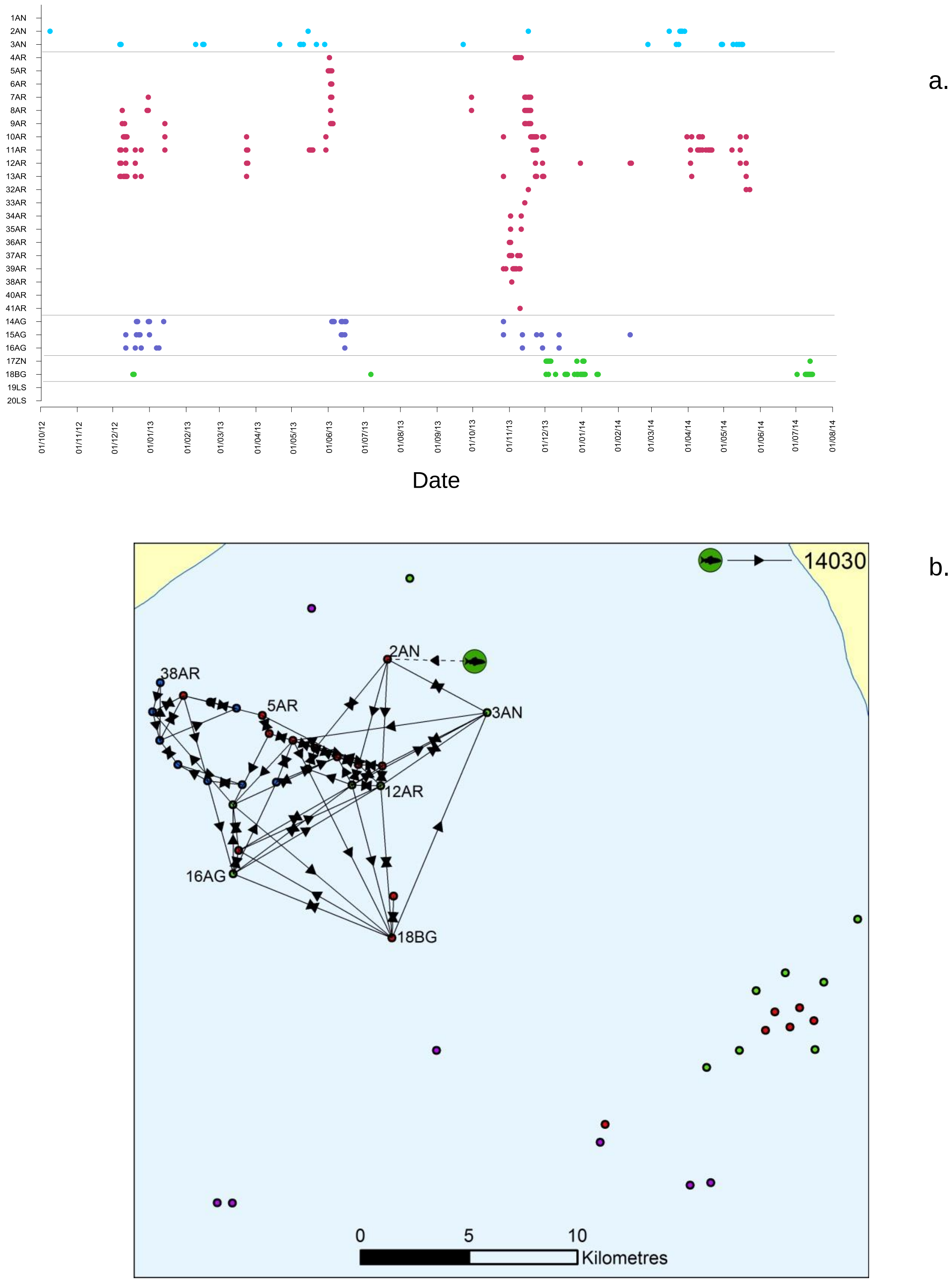


Fig. 5.19. Details of the movement behaviour of Fish 14030 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

5.4 Discussion

This chapter considered the space use and movement behaviour of snapper at the relatively small, within-region spatial scale in NGSV, using acoustic telemetry. Over the three years of the study up to 41 acoustic receivers were deployed throughout a study area of approximately 160 km^2. A total of 54 snapper, across a broad size range, were tagged with acoustic tags, with from 11 to 46 viable fish available at any one time. These fish provided a total of 521,544 detections within the study area and a further 23 recorded in south east Gulf St. Vincent. The results of the study can now be considered in terms of: the tractability of applying acoustic telemetry for snapper; describing the space use and movement behaviour of the fish; and placing these findings in a broad spatial and management context.

5.4.1 Tractability of methodology

The first objective of the study was to assess the tractability of applying acoustic telemetry to the study of movement behaviour of snapper. Our primary concern was that the large and very large fish that had not previously been considered in acoustic telemetry studies (Willis et al. 2001, Hartill et al. 2003, Parsons et al. 2003, Parsons et al. 2010), would not cope with being captured, anaesthetised and surgically implanted with an acoustic tag. Here, a total of 32 fish that were >60 cm CFL, including 17 fish that were equal to or greater than 80 cm CFL, were captured on commercial longlines and then implanted with different types of acoustic tags including the large V16 tags. From these, 29 fish (90.6%) were subsequently detected after a sufficient period to know that they had survived the capture and tagging process. Furthermore, from the 22 fish that were <60 cm CFL, there was no concern about the survival of 17 fish (77.3%), as detections were recorded some considerable period after tagging. The high numbers of detections recorded by numerous receivers and the detection periods of several years for some fish provide evidence of the success of the methods. These observations indicate that when snapper of a broad size range are handled carefully, which includes venting to relieve the symptoms of barotrauma, they are sufficiently robust to cope with the capture, surgery, external tagging, and treatment with antibiotics associated with acoustic tagging. As such, acoustic telemetry is a viable and tractable method for long-term movement studies for snapper of a broad size range.

5.4.2 Space use

Use of space by the tagged fish was considered by comparing the timing and duration of detections in the study area. No fish was detected continuously throughout its detection period. Rather, there was considerable variation in the frequency and duration of their visits that resulted in several categories of behaviour with respect to how the study area was used.

Temporary residents

'Temporary residents' were detected at the same station on a daily basis for several weeks up to four months at a time. This behaviour was only recorded at 17ZN, where the largely intact shipwreck of the Zanoni represents the largest submerged structure throughout NGSV, with its bow remaining intact and the stern post and rudder standing nearly six metres above the seafloor. Furthermore, this relatively sedentary behaviour of 'small' to 'medium' fish in the vicinity of the shipwreck was only recorded during winter and early spring. The high numbers of daily detections for these fish indicate that they did not venture far from the vicinity of the shipwreck. As such, at this time of the year, these fish were relatively sedentary, showed strong site fidelity, and had long periods of occupancy around the shipwreck. Also, there was considerable overlap in the space used by the individual fish. These findings are consistent with anecdotal reports from fishers that relatively small snapper remain close to the wreck (Lloyd pers. comm.).

The characteristics of limited and overlapping home ranges and strong site fidelity for small to medium-sized snapper were previously described from acoustic telemetry studies done in New Zealand (Willis et al. 2001, Hartill et al. 2003, Parsons et al. 2003, Parsons et al. 2010). The difference in findings between those earlier studies and this one is that the 'residential' behaviour of fish in NGSV did not persist into the warmer months. For these fish, the daily frequencies of detections declined through August and September, indicating that they spent less time each day associated with the shipwreck until early spring when the detections ceased. Most of these fish were only detected for one such prolonged period. Several of them, however, were recorded after they left 17ZN as having moved north to the AR and AN areas. This represented a significant seasonal change in behaviour that was associated with a habitat shift. Clearly, for such fish, the decline and ultimately the cessation of detections at 17ZN were behavioural (i.e. related to their purposeful seasonal departure from the vicinity of the shipwreck rather than them being captured by fishing).

Mobile, partial residents

The other behavioural category for which there were large numbers of detections for individual fish were the 'mobile, partial residents', which spent considerable periods of time in the study area. 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 behavioural category was not described from the movement studies undertaken in New Zealand (Willis et al. 2001, Hartill et al. 2003, Parsons et al. 2003, Parsons et al. 2010). All of these fish were >60 cm CFL and most were >80 cm CFL. They displayed seasonal variation in behaviour and areas used (Fig. 5.20). For periods during winter, some were detected daily at 17ZN. In this sense, their behaviour was similar to that of the 'temporary residents', although their stays at 17ZN were generally shorter. In spring, these fish moved and were detected throughout the AN, AR and AG areas, when these areas produced their highest detections rates. Some fish also visited the LS area during spring, where high numbers of detections were recorded until late summer. For periods of several weeks during these warmer months, during their daily activity these fish moved over areas that included several acoustic stations. As such, these 'local' movements were over greater distances than moved during winter.

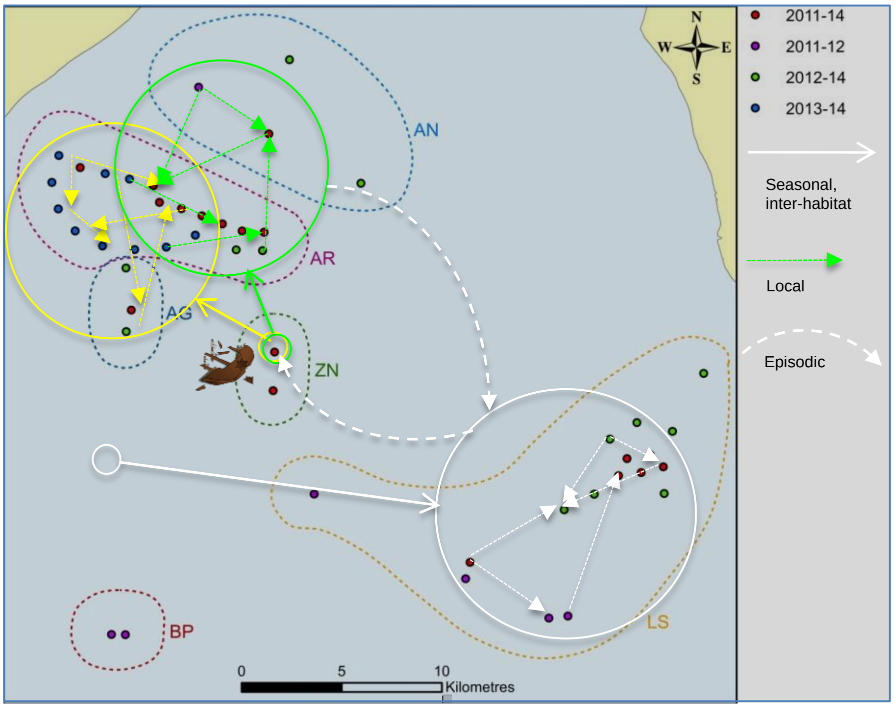


Fig. 5.20 Model of the movement behaviour of snapper in NGSV for three hypothetical fish (green, yellow, white). The figure depicts the areas occupied by each fish during winter and spring/summer and the direction of the 'seasonal, inter-habitat' movement between winter and spring. The 'local' and 'episodic' 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 a number of different stations, their activity was occasionally punctuated by a significant excursion to a different place (Fig. 5.20). Here, such excursions generally involved movement between areas, over distances of 10s of km in less than a single day. Sometimes the fish also completed the round trip back to the original site. This behaviour generally occurred prior to or during the reproductive season of snapper in the northern gulfs (Saunders et al. 2012), and so may have related to seasonal gonad maturation and reproductive behaviour. Movement studies for other species of large, demersal fish that generally have limited home ranges have demonstrated the spontaneous movement of individual fish over distances of 10s of km, to participate in spawning aggregations (Zeller 1998, Starr et al. 2007).

Transient, infrequent visitors

For the 'transient, infrequent visitors' there were very few detections recorded in the study area. As such, these fish only occasionally strayed into or passed through the study area. They were primarily 'large' fish. It is impossible to interpret these observations in any comprehensive description of movement. Nevertheless, their behaviour may not necessarily be different 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 some considerable distance from the study area (i.e., the scope of their movements may not have extended into the study area).

5.4.3 Movement behaviour

Several different types of movement behaviour by snapper were implicit in the patterns of space use, as characterised by the distances moved by the fish, timing of their movement and places involved (Fig. 5.20). These different movement behaviours can be categorised as: inter-regional; seasonal, inter-habitat 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 the gulf. These fish were responsible for moving over the longest linear distances between stations recorded in the study. Fish 14026 was captured, tagged and first recorded in NGSV, after which it was recorded along the Glenelg line of receivers and by the following year was back in 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 from where captured to the furthest site of detection was 64 km. For both fish, these are linear distances between detection points and therefore under-represent the actual distances that they would have moved during their detections periods. This indicates that there is exchange of individuals between the northern and southern parts of the gulf and that the population in NGSV is not an isolated, self-contained stock. In this sense it contrasts with the limited movement behaviour that is characteristic of the different gulfs that comprise Shark Bay in Western Australia (Bastow et al. 2002, Norriss et al. 2012).

At the smaller, within-region scale, the movement behaviour of small and large snapper varied seasonally. During winter, numerous fish were relatively sedentary and occupied the same station 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. These reports indicate that such schools are not necessarily always associated with the wreck of the Zanoni despite it being the largest structure in the northern gulf. The fish undergo a seasonal behavioural change associated with a habitat 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, as well as benthic invertebrates such as razorfish, bryozoans, sponges and ascidians (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 were distributed over areas that were sufficiently large for them to be detected by several acoustic receivers. Such ‘local’ activity concentrated in a particular area was occasionally interrupted by abrupt, episodic, movements over distances of 10s of km (Fig. 5.20). Such movements may have been associated with reproductive activity.

The findings of this acoustic telemetry study in NGSV can be considered in association with those from the historical tag/recapture studies (Jones 1981, 1984, McGlennon 2004) that were done in the northern gulfs to develop a general behavioural model. There are consistencies between studies, as well as additional information provided by each. The acoustic telemetry study 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 relatively sedentary for weeks to months. In late winter and spring, the schools dispersed. The subsequent behaviour may have been size-related. Few ‘small’ and ‘medium’ fish were detected throughout the study area during the warmer months, which is consistent with observations from earlier studies that the smaller fish move south and possibly leave the gulfs. In fact, one such fish tagged in NGSV was recaptured on the north coast of Kangaroo Island (Jones 1984). In contrast, in our study, most detections throughout the warmer months were of large and very large fish, which according to the earlier tagging studies tend to stay in the northern gulfs (McGlennon 2004). This acoustic telemetry study provided an insight into the behaviour of these fish for 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 based on external tagging identified that most recaptures across all size classes, including the 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 2004). 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.

5.4.4 Spatial management in Northern Gulf St. Vincent

South Australia’s snapper fishery has been subjected to considerable review and management changes in recent years that have been appropriately applied in NGSV. However, this regional fishery is also affected by some specific spatial conservation measures. The value of these various management measures can now be considered in the context of our enhanced understanding of the movement behaviour of snapper.

Soon after the discovery of the wreck of the Zanoni in 1983 it was declared an historic shipwreck under the *Historic Shipwreck Act 1981*. As a result, a 550 m protection zone was declared around the wreck from which vessels were precluded from entering. Furthermore, in October 2014, the Upper Gulf St. Vincent Marine Park became operational, which included The Offshore Ardrossan Sanctuary Zone (Fig. 5.21). The latter covers an area of approximately 40 km^2 from which fishing activity is excluded. It also includes the protection zone around the Zanoni from which all vessel activity remains excluded.

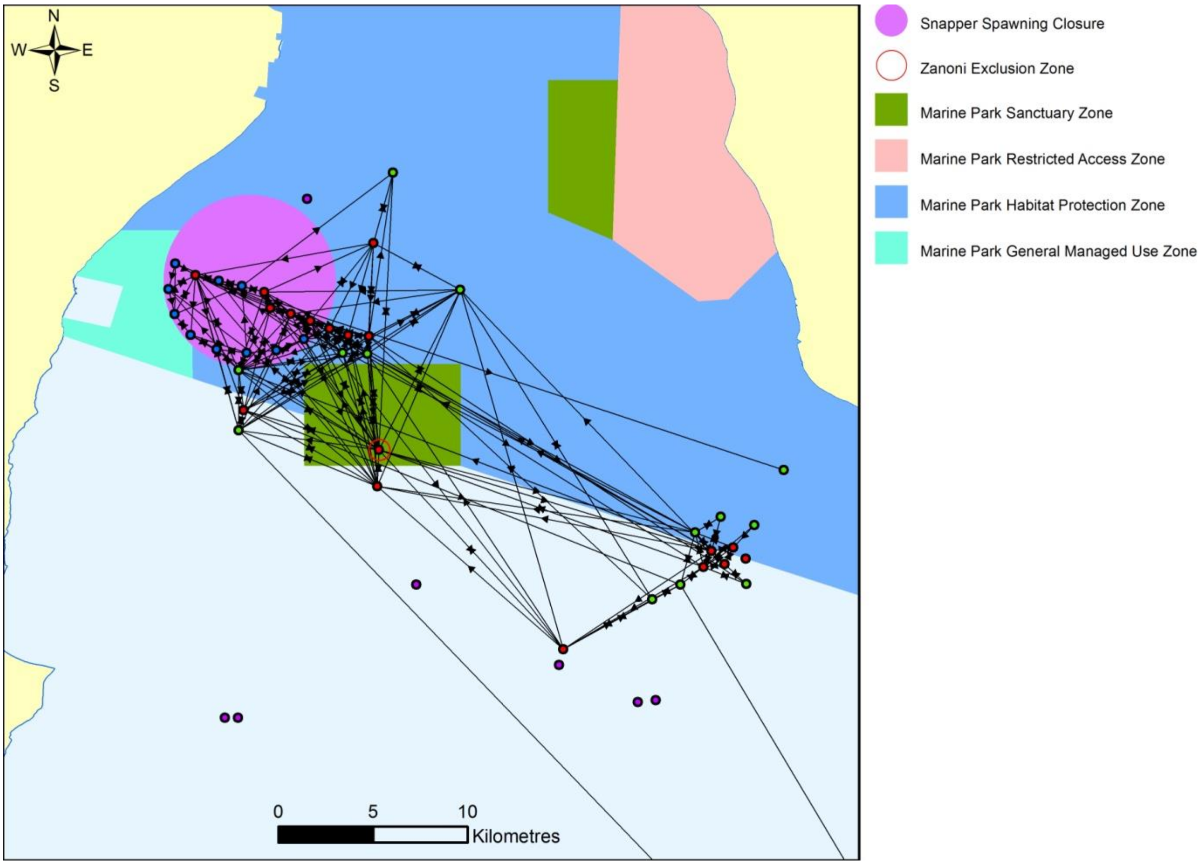


Fig. 5.21 Map of Northern Gulf St. Vincent showing the various spatial management zones including the new marine park zones, the snapper spawning spatial closure area and the Zanoni Exclusion Zone. The lines summarise the movements of snapper based on the 521,544 acoustic detections recorded over the three years of the acoustic telemetry study.

In addition, a series of recent management changes have been made for South Australia's snapper fishery. The strategic approach has been directed at limiting the impact of the commercial sector on the snapper stocks, whilst optimising the opportunities for local reproduction and recruitment (Fowler and McGarvey 2014). These measures included extending the seasonal, State-wide closure for snapper fishing for a further two weeks to cover the period from the 1 November to 15 December of each year. This period covers a significant part of the reproductive season of snapper in NGSV during which gonad development occurs and reaches its peak period of egg production (Saunders et al. 2012). One further management measure was the implementation of a spatial, spawning closure in NGSV from the end of the seasonal fishery closure on the 15 December until the 31 January in each year. This is a circular closure of 4 km radius, giving an area of approximately 50.3 km^2, which is located off-shore from the township of Ardrossan. The spawning spatial closure has now been implemented through the summers of 2013/14 and 2014/15 (Fig. 5.21).

In effect, the various spatial and temporal restrictions in NGSV should protect: all snapper during the period of 1 November to 15 December; all fish that occupy the approximate 40 km^2 of the sanctuary zone of the Upper Gulf St. Vincent Marine Park throughout the whole year, particularly those associated with the Zanoni; and the fish occurring in the spatial, spawning area from 15 December to 31 January each summer. The results of the acoustic telemetry study indicate that the exclusion of fishing activity from the shipwreck of the Zanoni would be highly beneficial for the NGSV snapper stock as it was the most important aggregation site within the study area that accounted for 67.8% of all detections. It was used for considerable periods by fish of a range of sizes during winter as well as large fish for shorter visits during the warmer months. In contrast, there is less certainty about the value of the spatial spawning closure in NGSV. Whilst several tagged snapper were recorded in the AR area from 15 December to 31 January, more detections were recorded there during spring and early summer than later summer, suggesting that this may not have been a significant spawning aggregation site through late December and January. Snapper egg surveys that were done in NGSV in December of 2014 and 2015, as part of FRDC Project 2014/019, may provide better resolved spatial information about the locations of spawning in this region.

5.4.2 Conclusions

Acoustic telemetry proved to be a useful and tractable method for studying snapper movement behaviour, even for the very large fish. There was considerable variation in snapper behaviour with respect to the frequency and durations of their visits to the study area. The ‘temporary residents’ were detected at the same station on a daily basis for several weeks to up to four months at a time. For the ‘mobile, partial’ residents there were large numbers of detections indicating that they spent considerable periods of time in the study area. Alternatively, the ‘transient, infrequent’ visitors only strayed into or passed through the study area. Several different types of movement behaviour by snapper were implicit in the patterns of space use, as characterised by the distances moved by the fish, the timing of their movements, and the places involved. These movement categories were: inter-regional; seasonal, inter-habitat different; local and episodic.

6. General Discussion

Anthony Fowler

Since 2007, South Australia's commercial snapper fishery has undergone major changes. These included an increase in annual State-wide catch to record levels up to 2012 that was associated with a significant change in the spatial structure of the fishery, in terms of the regional contributions (Chapter 1, Fig. 1.1). However, there was no understanding of the demographic processes on which these spatial changes in fishery production were based or the extent to which the events and processes that occurred in the different regions were related. This reflected our poor understanding of the movement behaviour of snapper and the extent to which it could influence regional population dynamics. This poor understanding also reflected uncertainty about the stock structure of snapper in south eastern Australia. Whilst there is evidence of broad-scale, genetic differences between the snapper populations of South Australia (SA) and Victoria (Donnellan and McGlennon 1996), the fine-scale stock division that is apparent in Shark Bay, Western Australia (Bastow et al. 2002, Norriss et al. 2012), warns of the possibility of fine-scale stock separation in the waters of south eastern Australia.

The need for this project was to enhance our understanding of the movement patterns and stock structure for snapper in south eastern Australia to determine the appropriate scale for and to inform the review of the strategy for management. The issues here relate to the locations of nursery areas where fish originated and their subsequent migration and replenishment of sink populations, which ultimately impacted on the regional patterns of population dynamics. Addressing such questions about fish movement over large spatial scales and influence on stock structure is often based on inferences that can be drawn from comparing phenotypic characteristics amongst regional populations (Pawson and Jennings 1993). This study used the recommended 'multiple-technique' approach (Begg and Waldman 1999, Hutchinson 2008) that focused on comparing numerous phenotypic characteristics amongst regional populations. The basic premise of this approach is - populations with similar phenotypic characteristics may experience sufficient exchange of individuals to represent a single stock. Alternatively, where phenotypic variation is apparent between populations, there may be sufficient separation for them to constitute separate stocks.

In this study, the phenotypic characteristics considered for snapper included the demographic and otolith characteristics of regional populations. The former involved: size and age structures; growth functions; and annual recruitment patterns. The latter were: otolith size; clarity of increment structure; as well as trajectories of increment widths, chemistry and optical density, measured across the chronological structure of TS-sections. The results from the various comparisons of phenotypic characteristics provided relatively consistent results and allowed the proposal of hypotheses regarding the recent changes in regional fishery production, as presented below.

6.1 Regional trends and demographic processes

6.1.1 South East Regional Population

The snapper population of the South East (SE) region of SA experienced dramatic, exponential increases in annual commercial catches and catch rates between 2007 and 2012. The annual regional catch increased from just a few tonnes in 2005 to a peak of 258 t in 2010, reflecting a significant increase in regional biomass. The issue for this regional population was – where did the fish come from that accounted for this higher biomass?

The total reported commercial catch from this region across the six years of 2007 to 2012 was 774 t. The increase in population size to support this catch must have involved many hundreds of thousands of fish. It is unlikely that there is a nursery area located along the south eastern coastline of SA that could produce sufficient juvenile fish to disperse throughout and raise the regional biomass to such an extent. Nursery areas for snapper are usually protected waterways such as the large embayments and gulfs of western Victoria, SA, Western Australia, and New Zealand, and the coastal estuaries of eastern Victoria and New South Wales (Gillanders 2002, Fowler and Jennings 2003, Hamer and Jenkins 2004, Wakefield 2010, Dias et al. 2015). Such habitats do not occur along the exposed coastal fringe of the SE. Rather, there are three primary nursery areas throughout south eastern Australia that could produce sufficient recruits to supplement the SE population (Fowler and Jennings 2003, Fowler et al. 2005, Hamer et al. 2011). However, these nursery areas (i.e. Northern Spencer Gulf (NSG), Northern Gulf St. Vincent (NGSV), and Port Phillip Bay (PPB)), are considerable distances from the SE, and would require mass emigration of fish over distances of 100s of km. Whilst there are tag/recaptures indicating that individual snapper can move such distances (Moran et al. 2003, McGlennon 2004), including throughout south eastern waters (Coutin et al. 2003), to date there is no evidence of mass emigration of snapper over such distances. As such, the question for this region becomes – is there evidence from the inter-regional phenotypic comparisons to support the hypothesis of recruitment to the SE from one of the three potential source populations?

The snapper population of the SE involved truncated size structures compared to the gulf regions (Fowler et al. 2013). These reflected slower growth rates and truncated age structures thereby representing major demographic differences compared with the populations in the gulf regions. Also, their otoliths were less clear than those from the northern gulfs. Ultimately however, evidence from the TS-sections of the otoliths pointed to the origins of the SE fish. The results from increment width and otolith chemistry analyses for these fish were overwhelming in their similarity to the otoliths from PPB. The elevated levels of Ba, a characteristic of otoliths from PPB

(Hamer et al. 2006), as well as for Sr, Mn and Mg in the first few increments were almost identical to the chemical signature of the PPB otoliths. These similarities between regions suggest that fish from the 2001 and 2004 year classes captured in the SE had originated in PPB. Furthermore, the trajectories of chemistry and increment widths across the chronological structure of the otoliths from the SE and PPB began to diverge from the 1-2 increment onwards, with the differences particularly strong for the 4-5 and 5-6 increments. This divergence is consistent with fish that were captured in the SE leaving PPB and moving the 600 km westward through western Victorian coastal waters. The gradual, age-related divergences of physical and chemical characteristics of the otoliths from the two regions suggest that all fish did not leave PPB in synchrony, but that their departures were staggered over a few years. Since the 2001 and 2004 year classes were not evident in the regional catches in the SE until five or six years after their birth year, suggests that the completion of the 600 km journey may have taken several years.

The results of this study strongly suggest that the population dynamics in the SE and episodic nature of this regional fishery were driven by recruitment variability in PPB, followed by mass emigration from the bay and long-distance dispersal to the SE, possibly over several years. Findings from several other studies support this model of population replenishment. First, a trawl survey has been done annually for 0+ snapper in PPB since 1992/93 (Hamer and Jenkins 2004, Kemp et al. 2012) that has provided 23 consecutive annual estimates of recruitment rates. There were two years that produced exceptional numbers of 0+ snapper (i.e. 2001 and 2004). As year class strength for snapper is established in the very early life history (Zeldis et al. 2005, Murphy et al. 2012, 2013), the high numbers of 0+ recruits for 2001 and 2004 are considered genuine indicators of year class strength. These two strong year classes correspond with those in the age structures of the SE between 2007 and 2012. The departure of juvenile fish from PPB may have been a density-dependent process that was driven by high numbers of juvenile fish that result from the strong recruitment. Previous otolith chemistry studies identified PPB as the primary source population for recruits to the snapper populations in western Victorian waters (Hamer et al. 2005, 2006, 2011). This study has provided empirical evidence for the extension of the western boundary of the Western Victorian Stock into South Australian waters.

6.1.2 Southern Gulf St. Vincent Regional Population

The annual commercial catches of snapper from Southern Gulf St. Vincent (SGSV) have historically been approximately an order of magnitude lower than for NSG, SSG and more recently for NGSV (Chapter 1, Fig. 1.1). Nevertheless, the relatively low regional catches increased marginally between 2007 and 2012, in synchrony with the higher catches from NGSV and the SE, suggesting a marginal increase in biomass. Furthermore, the demographic characteristics of this regional population changed considerably over time. In 2001 to 2003, the population was dominated by ‘large’ and ‘very large’ snapper. Alternatively, from 2009 to 2011, i.e. the period of higher catches, the population was dominated by ‘small’ and ‘medium’ fish. The truncated size structures from the latter period were associated with a growth function that had a considerably lower L_∞ value than earlier in the 2000s. The age structures in both periods were dominated by a single year class (i.e. the 1991 year class for the former and the 2001 year class in the latter period). The primary demographic questions for this region were - from where did the strong year classes originate and why did the demographic characteristics change so considerably through the 2000s?

The physical and chemical characteristics of otoliths from SGSV produced surprising results with respect to the sources of recruitment. For the 2001 year class, there were similarities in increment widths and chemistry of the first few increments in the otoliths from SGSV, PPB and the SE, which led to the conclusion that the fish from SGSV had also originated in PPB. These fish would have completed an even longer westward journey from PPB than did those that recruited to the SE. The lower abundance in SGSV compared to the SE, suggests that fewer fish achieved this greater distance of travel. These fish most likely represented the westward extent of the Western Victorian Stock.

In contrast, the otoliths from the 2004 year class from SGSV suggested an entirely different geographic source of recruits. The chemistry of the first few annual increments was more similar to that for fish from the northern gulfs than PPB. Furthermore, the physical and chemical characteristics of otoliths from the strong 1991 and 1997 year classes also excluded PPB as the source population for SGSV. Rather, for the latter year class in particular, otolith chemistry pointed to NSG as the most likely source, which is consistent with NSG having a higher spawning biomass than NGSV at that time, and so greater potential for egg production (Fowler et al. 2013).

This study has determined that the 2001 year class from SGSV, most likely originated in PPB, and had moved into SGSV, representing a westward extension of the Western Victorian stock. Alternatively, fish from the 1991, 1997 and 2004 year classes had originated in one of the northern gulfs. This makes for a complex stock structure in SGSV, establishing it as a mixing zone for fish originating from different nursery areas. That the different year classes came from different nursery areas contributes to the differences in size structures between the early and late 2000s. Through the first period, the size structures were dominated by ‘large’ fish, predominantly from the 1991 year class. Such ‘large’ fish of approximately 10 years of age were also evident in NGSV, SSG and NSG, suggesting that adult fish moved into SGSV. In contrast, in 2009-11, the higher catches from SGSV involved much smaller fish that were dominated by the 2001 and 2004 year classes. The different geographic origins of these two year classes affected their growth rates. The 2001 fish from SGSV were small compared to similar-aged ones from the SA gulfs, reflecting their low growth rates due to their movement through low temperature coastal waters of western Victoria and south eastern South Australia. The 2004 fish had originated from one of the gulfs and had higher growth rates than the 2001 fish. As such, in 2009, the sizes of these younger fish largely overlapped with the older fish from the 2001 year class.

6.1.3 Northern Gulf St. Vincent Regional Population

Historically, Northern Gulf St. Vincent (NGSV) produced relatively low catches of snapper of <20 $t.yr^{-1}$ (Chapter 1 Fig. 1.1, Fowler et al. 2013). However, from 2003, the annual catches began to increase, slowly at first and then more rapidly. The annual catch was 37 t in 2005, 66 t in 2007, 193 t in 2009, and then peaked at 414 t in 2012. This substantial change in catch was associated with an increasing catch rate that reflected both the adoption of new, efficient longline fishing technology, as well as a simultaneous increase in regional, fishable biomass (Fowler et al. 2013). Since this regional snapper fishery is the primary one that maintained the State-based catches through the late 2000s, one of the most significant objectives of this project was to determine the source of this increase in biomass. There were several alternative hypotheses. NGSV is one of the primary nursery areas of south eastern Australia (Fowler et al. 2005), and so the recent high biomass may have gradually accumulated through local reproduction and recruitment. Alternatively, large numbers of snapper may have moved into NGSV from elsewhere, with the likely sources being the two other primary nursery areas in NSG or PPB.

The otolith analyses were informative about the origins of the NGSV population. First, the strong 2001 year class in SGSV that had originated in PPB raised the possibility that such fish may have also moved into and supplemented the population in NGSV. However, the otoliths from NGSV did not display the high Ba signal that is characteristic of PPB. Furthermore, their otolith increment structure was clearer and more easily interpreted than for PPB, SE and SGSV. Overall, these differences in otolith characteristics indicated that snapper that moved to SGSV from PPB did not continue up the gulf and supplement the population in NGSV. The otolith analyses for the 1991, 1997 and 2004 year classes were also consistent in providing evidence for the lack of movement from PPB to NGSV.

There remained the possibility that juvenile or adult snapper migrated from NSG to NGSV. For both the 2001 and 2004 year classes, there were no differences in otolith chemistry between fish from NSG and NGSV. Such similar data are not useful in this context as they are consistent with the two alternative hypotheses about the origins of the NGSV fish (Campana 1999). However, there were relatively subtle regional differences in the age-related trends in elemental concentrations for the 1991 and 1997 year classes that were more useful in this context. These age-related data suggested that if fish from NGSV had originated in NSG, they must have undertaken this significant movement in the first one or two years of life. Although young snapper are capable of moving considerable distances (McGlennon 2004), it is highly unlikely that there was mass movement of juvenile fish over the approximate 500 km between NSG and NGSV, crossing through numerous different ecosystems. Rather, it is more likely that NGSV is a separate population from NSG, with independent processes driving the population dynamics. The findings from several different independent studies support this conclusion. The results from numerous tag/recapture studies that were done for snapper between 1977 and 1992 showed that most recaptures were made within 20 km of the tag/release sites for up to several years after being tagged (Jones 1981, 1984, McGlennon 2004). Whilst some snapper were recaptured up to several hundred km from their tag sites, including some that moved either from Spencer Gulf or Gulf St. Vincent into Investigator Strait, there was no record of any tagged snapper that moved from Spencer Gulf into Gulf St. Vincent, or in the opposite direction. This supports the hypothesis of separate populations in NGSV and NSG.

The results from a further study supported the hypothesis of separate populations occupying NGSV and Spencer Gulf. This was a recently-completed Honours research project that compared the head and jaw morphology as well as otolith shape between snapper collected from the different South Australian gulfs (Rogers 2014). The study was based on work done inter-state and in New Zealand that demonstrated that snapper from different stocks can display considerable differences in head shape and jaw morphology (Moran et al. 1998, Parsons et al. unpublished data). Furthermore, the analysis of otolith shape has emerged as a significant tool in stock discrimination studies (Steer and Fowler 2014, Vieira et al. 2014). For South Australian snapper, the study demonstrated clear and significant regional differences in head shape, jaw morphology and otolith shape. Between NGSV and NSG, clear differences were apparent even for fish of <50 cm CFL, i.e. approximately six years of age or less. For such regional differences to be manifested for relatively young fish, they must have already been living in different places with different environmental characteristics for numerous years. Such data are consistent with no significant migration of sub-adult or adult snapper between NSG and NGSV, which again suggests separate populations.

The conclusion that NGSV supports a separate population that is not replenished from either NSG or PPB implies that the biomass of this region through the late 2000s built up through local processes of recruitment and replenishment. The age structures and resulting recruitment history indicate numerous strong year classes that recruited to the population both during the 1990s and 2000s (i.e. 1991, 1997, 1999, 2002, 2004 and 2006). Presumably the 1991 year class was the source for the 1997 and 1999 year classes which then gave rise to the subsequent strong year classes of the 2000s. The persistence of the 2001, 2004 and 2006 year classes in the population represents a significant point of difference with the regional populations in Spencer Gulf.

6.1.4 Southern Spencer Gulf Regional Population

Historically, Southern Spencer Gulf (SSG) has been the second most significant regional contributor to SA's snapper fishery behind NSG. From 1984 to 2007, these two regions dominated the State's commercial catches. For SSG, there were two periods of particularly high production (i.e. 1999 - 2002 and 2005 – 2009) for which the fishery statistics suggest high levels of biomass (Chapter 1 Fig. 1.1, Fowler et al. 2013). Furthermore, during the second period, the use of new efficient longline fishing technology was introduced, which significantly increased the catch rates of the fishers. However, following the highest annual catch for this region in 2007, there were dramatic declines in regional catches and catch rates to 2013 that were strongly indicative of a declining fishable biomass (Fowler and McGarvey 2014). The significant fishery question for this region is - why did the biomass decline so dramatically after 2007? To address this, it is necessary to understand the demography of the region with respect to the processes of population replenishment.

The physical and chemical characteristics of the otoliths from SSG for the 1991, 1997, 2001 and 2004 year classes were different to those from PPB, indicating that it was highly unlikely that the Western Victorian Stock extended into SSG. Rather, the characteristics of the first few increments of the otoliths were similar to those from NSG and NGSV, indicating that one of these regions was the likely source population. In the 1990s, there was a much higher biomass of snapper in NSG than NGSV, thus providing greater potential for egg production (Fowler et al. 2013). Furthermore, the proximity and geographic continuity between NSG and SSG provides greater likelihood that NSG was the source population. For the 1997 year class, the trends in elemental profiles in the otoliths differed between SSG and NGSV, providing further evidence that NSG was the likely source population. NSG also had higher biomass and greater potential for egg production in that year.

The hypothesis proposed above suggests that NSG is the primary source of recruitment to SSG, with immigration occurring from a few years of age. This model is supported by results from historic tag/recapture studies that showed numerous fish, mainly of only a few years of age, moving from NSG to SSG, over considerable distances (Jones 1981, 1984, McGlennon 2004). There is also evidence that some fish moved back into NSG from SSG. Consequently, it is likely that there is considerable exchange of adult fish between the two regions that accounts for their similar size and age structures.

The hypothesis for replenishment of the regional population of SSG strongly links the population dynamics of that region with demographic processes in NSG. The two regions shared the same strong year classes of 1991, 1997 and 1999. In fact, these year classes were even stronger in SSG, which may reflect that relatively more fish from strong year classes move south from NSG as a consequence of density-dependent processes. Furthermore, evidence for inter-related demographies lay in the considerable synchronicity in the declines in fishery productivity of the two regions. The declining biomass in both regions through the 2000s reflected the lack of recruitment of a persistent, strong year class to either SSG or NSG. The proposed immigration of young fish to SSG from NSG indicates that the two regions should be considered component regional populations of a single stock.

There is one clear difference between the population characteristics of SSG and NSG. In the former region, the size range of fish for each age class was particularly broad as many fish were small for their ages. This culminated in low estimates of L_∞, and broad confidence limits around the estimate of K. The existence of these fish does not preclude there being a strong interaction between the populations of NSG and SSG. The 'stunted' inhabitants of SSG may have become residents of this region after their emigration from NSG. At the same time, the larger fish in SSG may be more mobile and spend at least part of their lives in NSG, where growth rates are significantly higher due to the higher water temperatures and different food taxa (Lloyd 2010).

6.1.5 Northern Spencer Gulf Regional Population

Despite its relatively small area, Northern Spencer Gulf dominated SA's fishery catches between 1984 and 1999 (Fowler et al. 2013). Likely contributing factors to this high productivity are; the region includes a large nursery area (Fowler and Jennings 2003) and several significant spawning aggregations sites, and also supports an abundance of the preferred prey taxa of blue swimmer crabs (*Portunus armatus*) (Lloyd 2010). Nevertheless, the catches declined from 2002, and by 2013 had fallen to their lowest ever level (Fowler and McGarvey 2014). Our otolith analyses provided no evidence of any supplementation of this regional population from either of the other two primary nursery areas of PPB or NGSV. As such, this regional population is considered to be self-recruiting through local reproduction. Furthermore, the nursery area has been implicated in supporting, through emigration, the regional populations of SSG, SGSV (this report), as well as the snapper population of the west coast of Eyre Peninsula (Fowler et al. 2005). As such, the primary demographic question for this region is – why did the biomass decline to a fraction of what it was 15 years ago (Fowler and McGarvey 2014)?

Fishery production in NSG has varied cyclically since 1984, reflecting the influence of inter-annual variability in recruitment (Fowler and McGlennon 2011, Fowler et al. 2013). A decline in productivity to 1994 reflected poor recruitment through the 1980s, whilst the subsequent increase in fishing catch to the record levels of 1999 to 2002 reflected the impact of recruitment of the strong 1991, 1997 and 1999 year classes (Fowler and McGlennon 2011). As such, these three year classes dominated the age structures in the early 2000s. However, in the late 2000s, when fishery catches and catch rates eventually dropped in 2012 and 2013 (Fowler and McGarvey 2014), the annual age structures continued to be dominated by the 1997 and 1999 year classes. This indicates that for NSG there has been no recruitment of a significant year class since 1999. Nevertheless, through this prolonged period of poor recruitment, fishing effort remained relatively high (Fowler et al. 2011). Furthermore, because of the aggregative behaviour of snapper and the knowledge and expertise of the local fishers, the catch rates also remained high, despite the diminishing biomass. This situation of 'hyperstable' catch rates persisted until the regional fishery catch crashed in 2012, after which it has remained low (Fowler and McGlennon 2011). It appears that the biomass in NSG has fallen due to the failure of recruitment since 1999 and the depletion of adult spawning biomass through the continuation of fishing. This regional failure of recruitment to the primary nursery area in NSG has also contributed to the fall in biomass in SSG and possibly also impacted on the biomass and fishery productivity in SGSV and the west coast of Eyre Peninsula.

6.2 Movement behaviour

Until recently, understanding about the movement behaviour of snapper in south eastern Australia was largely based on findings from tag/recapture studies (Jones 1981, 1984, Coutin et al. 2003, McGlennon 2004). Those studies provided an invaluable basis that can now be enhanced from the findings of our acoustic telemetry and otolith studies. The numerous historic movement studies done in SA, which involved the tagging of >13,000 snapper and ~850 recaptures (Jones 1981, 1984, McGlennon 2004), provided some consistent results. Most recaptures were made within only a few km from where the fish were tagged, suggesting only relatively local movement. However, a much smaller proportion of recaptures were taken up to several hundred km from their tag/release sites. Consequently, snapper were differentiated into 'residents' and 'migrants', based on the spatial extent of their movements (McGlennon 2004). Such findings were consistent with those from similar studies done inter-state in Australia (Coutin et al. 2003, Moran et al. 2003, Sumpton et al. 2003, Norriss et al. 2012) and New Zealand (Paul 1967, Crossland 1976, Willis et al. 2001).

It was apparent from historic tagging studies in SA that the scale and direction of fish movement were related to fish size and age (McGlennon 2004). Small fish of 20 – 40 cm CFL moved over the greater distances and were generally southward-directed away from the nursery areas in the northern gulfs. In contrast, the movements of fish >60 cm CFL were generally directed northwards, whilst the largest fish tended to remain resident to the northern gulfs. Such results suggested that the dispersion of snapper is not consistent across size and age classes, but that population structure varies spatially due to age-related movement behaviour. In support of this, the northern gulfs typically have broader size and age distributions that involve higher numbers of large, old snapper than do the southern regions (Fowler et al. 2013).

The current study, particularly the results from the otolith chemistry analyses, demonstrated that such inter-regional movement can have profound demographic and ecological implications. This significance is evident in the mass emigration events that occur over distances of hundreds of km that can ultimately drive the regional patterns of population dynamics and fishery productivity. The clearest example of this was the movement of young snapper from PPB that ultimately supplemented regional populations in SA. This process must have involved many 1000s of young fish that moved distances of 600 km or more, some of which even travelled further and reached the southern Fleurieu Peninsula of SGSV. Fish that completed these long migrations then sustained fishery catches for numerous years. At this stage it is unknown whether such fish persisted in the SE or whether, on reaching sexual maturity, some returned to PPB to re-join the adult spawning stock. Nevertheless, the 2001 and 2004 year classes persisted in the SE until 2014, until they were at least 13 years of age.

There were other regional populations that were also impacted by such mass emigration events. These included movement of individuals from the strong 1991, 1997 and 1999 year classes from NSG to SSG, as well as from the 1997 year class from NSG to SGSV. Furthermore, an earlier otolith chemistry study indicated that it was likely that some fish from the strong 1991 year class from NSG also left the gulf and supplemented the snapper population of the west coast of Eyre Peninsula (Fowler et al. 2005). Some of these fish persisted in west coast waters at least up to 2009, when they were 18 years of age. This process of regional supplementation through movement of large numbers of juvenile fish is synonymous with emigration of snapper from PPB and their recruitment to regional populations of western Victoria and south eastern South Australia (Hamer et al. 2005, 2006, 2011). This model of regional supplementation from particular nursery areas also appears to be the case for the snapper populations of southern Western Australia (Wakefield et al. 2011, Fairclough et al. 2013).

The acoustic telemetry study that was concentrated in NGSV also provided evidence of inter-regional movement over distances of ~100 km. Nevertheless, the real significance of this acoustic telemetry work lay in the insights provided about intra-regional movement over the spatial scale of metres to 10s of km. Our understanding of the movement behaviour of snapper at this relatively small spatial scale for Australian populations of snapper is poor due to the limitations of the earlier studies. The acoustic telemetry work clearly demonstrated that the movement behaviour of snapper was not random and that the activities of individual fish were spatially restricted and demonstrated systematic seasonal change. During winter, the fish were thigmotaxic, i.e. associated with structure on the seafloor, and largely sedentary, forming large, non-mobile aggregations around structures such as the Zanoni shipwreck. Through this season, numerous fish were detected for several months at the same station, suggesting limited ranges of movement. However, their behaviour changed during spring and summer. The schools dispersed as the fish became more active and engaged in ‘seasonal, inter-habitat’ movement whereby they moved north to areas that supported different benthic habitats. Such inter-habitat movement was not evident in the previous small-scale, behavioural studies for snapper that were done in New Zealand (Parsons et al. 2003, 2010, Egli and Babcock 2004). In NGSV through the warmer months, the activities of individual fish were focussed in a few centres of activity in particular areas that were considerably larger than those used during winter. There was also considerable overlap in the areas used by different individuals. Through the warmer months some fish also undertook ‘episodic’ movements over distances of 10s of km in just a few days.

Overall, the acoustic telemetry study revealed a complexity of different types of behaviour that were classified as ‘seasonal, inter-habitat’, ‘local’, and ‘episodic’. These operated at different temporal scales and encapsulated seasonal changes in mobility, size of area and habitat used, possibly in relation to food resources and reproduction. The repeated patterns of behaviour revealed that snapper are highly mobile with refined skills of navigation over distances of 10s of km and areas of at least 160 km^2.

6.3 Conclusions

6.3.1 Life history and stock structure

Our enhanced understanding of the movement behaviour of snapper and its demographic significance allows us to reconsider our understanding of the life history of snapper and how it relates to the stock structure throughout south eastern Australia. To date, two variations of the life history have been proposed (Fowler 2008). The first originated from tag/recapture studies and comparative regional characteristics (McGlennon and Jones 1997). This model largely emphasised the significance of annual, age-related migration from the gulfs to the continental shelf to account for differences in regional population characteristics. A second life history model that was developed from the earlier otolith chemistry study (Fowler et al. 2004, 2005), proposed that the two northern gulf populations were the sources of recruits that eventually migrated to and replenished other regional populations. Neither of these two earlier life history models was sufficiently comprehensive to account for the recent changes in SA's snapper fishery. Now, with our enhanced understanding of fish movement from this study it is possible to develop a more spatially-explicit life history model.

There is evidence for three primary nursery areas for snapper throughout the south eastern region of Australia, i.e. NSG, NGSV and PPB (Fowler and Jennings 2003, Hamer and Jenkins 2004, Fowler et al 2005). Each source population is not only self-sustaining but provides recruits that subsequently emigrate to and replenish adjacent and other regional populations. The numbers of fish available for such emigration depend on the inter-annual variation in recruitment that is characteristic of the populations of this broad geographic region (Fowler and Jennings 2003, Hamer and Jenkins 2004). Furthermore, the extent of movement influences the stock structure. PPB is the primary source of recruits for the snapper populations of western Victoria (Hamer et al. 2005, 2006, 2011) and the SE of SA (Fig. 6.1). These emigrants move as far west as the Fleurieu Peninsula in SA. It is now apparent that the westward extent of this movement, the sizes of these local populations and episodic nature of the regional population in the SE are driven by year class strength, as determined by recruitment variability in PPB.

Variable recruitment is also characteristic of the populations of NSG and NGSV (Fowler and Jennings 2003, Fowler et al. 2010). The former region is considered the primary source of recruitment to SSG through large-scale movement. Furthermore, when abundances were higher during the early 2000s (Fowler et al. 2013), NSG was probably also an important source of recruits for both Investigator Strait and the west coast of Eyre Peninsula (Fowler et al. 2005) (Fig.

6.1). As such, in the past, population abundance and recruitment variability in NSG are likely to have been significant drivers of population dynamics and structure in both regions. Nevertheless, there appears to not have been significant movement of fish from NSG to NGSV. The latter region appears to support a self-sustaining population whose recent significant biomass built up through local reproduction and recruitment. The lack of movement of fish in either direction between NSG and NGSV may reflect a tendency for fish to return to their natal areas and the refined navigational skills that they use to achieve this.

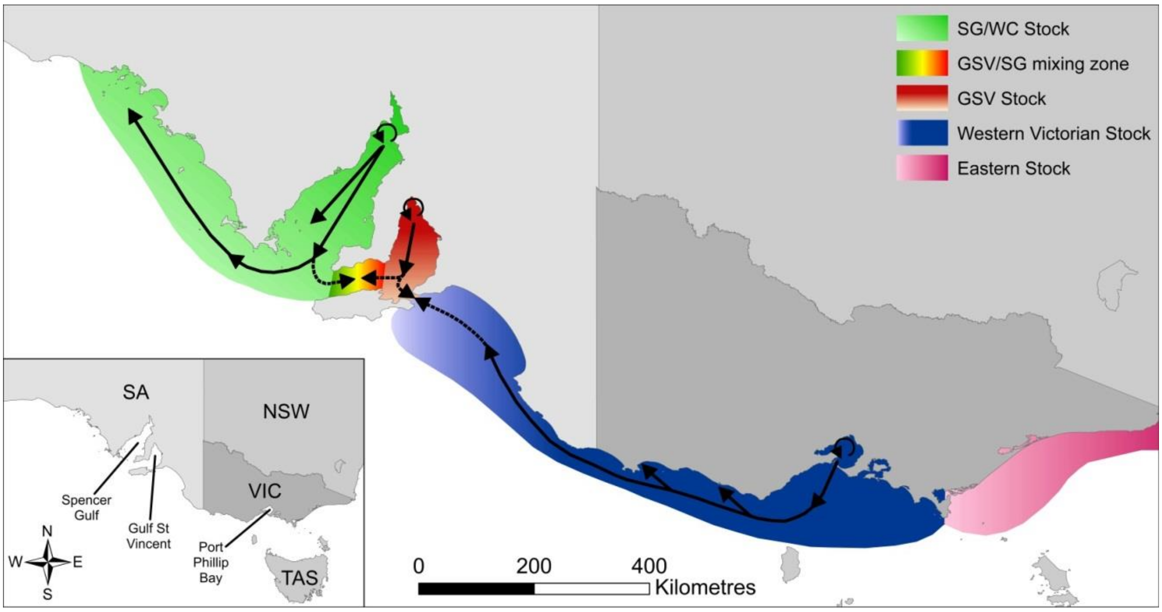


Fig. 6.1 Map of the coast of south eastern Australia, showing the stock structure for snapper, based on findings about movement from this study. The arrows indicate the directions and extent of emigration of fish from the three primary nursery areas in Northern Spencer Gulf, Northern Gulf St. Vincent and Port Phillip Bay, Victoria. Inset shows the broader geographic region. SG- Spencer Gulf, GSV – Gulf St. Vincent, WC – west coast of Eyre Peninsula.

The stock structure for snapper is built around the three primary nursery areas and the subsequent emigration from them. PPB is the primary source of recruitment to the populations of western Victoria and SE SA. This Western Victorian Stock extends westward from Wilsons Promontory, Victoria to as far as the Fleurieu Peninsula in SA (Fig. 6.1). Nevertheless, the westward extent of movement of these fish varies amongst year classes, possibly based on year class strength and the time since recruitment. Whilst Spencer Gulf is divided into northern and southern regions for stock assessment and reporting purposes, the biological data indicate that there is considerable exchange of individuals between these regions that include emigration from NSG to SSG, as well as annual north/south migrations. As such, these regional populations constitute a single stock (Fig. 6.1). Furthermore, it is likely that in the past, emigration from NSG replenished the populations of the west coast of Eyre Peninsula and Investigator Strait (Fowler et al. 2004, 2005). The lack of evidence of movement of fish from either PPB or Spencer Gulf into

Gulf St. Vincent, suggests that the latter region supports a separate stock (Fig. 6.1). Given the mobility of some snapper, it is likely that the boundary areas between the different stocks will involve overlap of individuals from different natal origins. Investigator Strait is likely to support snapper from both gulfs, whilst the waters of southern Fleurieu Peninsula may involve a mixture of fish from all three different stocks. Overall, the empirical data suggest that from a management perspective the snapper population of south eastern Australia is divisible into the Western Victorian Stock, Gulf St. Vincent Stock and Spencer Gulf / West Coast Stock (Fig. 6.1).

6.3.2 Conclusions against objectives

The objectives of this project were successfully achieved, as indicated by the key findings and outcomes below.

Objective 1: to determine the spatial origins of snapper that occupy the different regions of South Australian waters, and determine if and when during their life histories that any large-scale movement took place to account for current patterns of dispersion. This was primarily based on a suite of otolith-based techniques.

- The regional populations of SA constitute three stocks, i.e. the Western Victorian, Gulf St. Vincent and Spencer Gulf / West Coast Stocks which are each dependent on a significant nursery area.
- Each snapper stock consists of a number of adjacent regional populations that are replenished through inter-annually variable recruitment to the significant nursery area. The latter is an important source from which large numbers of juvenile and adult snapper subsequently immigrate and disperse throughout the regional populations.
- The snapper population in the SE supports an episodic fishery that is part of the Western Victorian Stock and depends on recruitment into and subsequent emigration from PPB, Victoria. NSG and NGSV each support self-recruiting populations. SSG depends on emigration from NSG, whilst SGSV is a mixing zone for fish from the three nursery areas.

Objective 2: to develop a better understanding of the movement behaviour of snapper at several spatial and temporal scales throughout Northern Gulf St. Vincent, using acoustic telemetry techniques.

- Acoustic telemetry proved to be a viable method for snapper and provided insights into their movement behaviour over the spatial scale of up to 10s of km;
- Snapper movement behaviour was not random, but rather was systematic as fish visited the same places at the same times of the year, and also demonstrated systematic seasonal differences.
    - In winter, snapper formed large, non-mobile aggregations around significant habitat structure.

- After winter, snapper undertook significant seasonal, inter-habitat movement, and the schools dispersed as the fish became more active.
- During the warmer months, the fish occupied particular areas that were larger than during winter.
- Snapper demonstrated four types of movement behaviour based on timing and distances moved, i.e. 'episodic', 'local', 'seasonal inter-habitat', and 'inter-regional'.
- Snapper proved to be highly mobile, capable of moving over distances of 10s of km, and had refined skills of navigation evident in their revisiting the same places distributed throughout areas of at least 160 km^2.

Objective 3: to develop a better spatial management strategy for the snapper fisheries of south eastern Australia based on our enhanced understanding of inter-regional and cross-jurisdictional fish movement.

- In SA, significant changes to the management regime have been made in recent years. These changes recognise the significance of the spawning aggregations and the need to ensure recruitment to the particular nursery areas in NSG and NGSV.
- Furthermore, as the population dynamics and stock structure of snapper are now better understood, the stock assessment and reporting processes in SA will be modified appropriately.
    - This will include a significant revision in 2018 of the harvest strategy in the Management Plan.
    - Changes to the spatial structure of the assessment and reporting processes which will include an assessment of the spatial structure considered in the computer stock assessment model.

7. Implications

This research project has culminated in hypotheses regarding the demographic processes that drive the temporal dynamics, including recent unprecedented changes, for each regional population in SA's snapper fishery. Fundamentally, the population dynamics are driven by inter-annual variation in recruitment to the three primary nursery areas of Northern Spencer Gulf (NSG), Northern Gulf St. Vincent (NGSV) and Port Phillip Bay (PPB), Victoria. The other regional populations depend on supplementation through emigration of juvenile and/or adult fish from these source populations. The South East (SE) region depends on recruitment into and emigration from PPB. Southern Spencer Gulf (SSG) and probably also the west coast of Eyre Peninsula (WC) are similarly dependent on NSG, whilst Southern Gulf St. Vincent (SGSV) depends on movement from NGSV. Investigator Strait is a likely mixing zone for recruits from each of NSG, NGSV and PPB.

The patterns of movement of juvenile and adult fish determine the stock structure in south eastern Australia. The different nursery areas and lack of emigration of fish between Spencer Gulf (SG), Gulf St. Vincent (GSV) and the SE indicate that each constitutes a separate stock. As such, this identifies the spatial scale at which fishery management and monitoring can be directed without there being broader scale impacts. Although there are already some regional differences in the current management harvest strategy, these were not based on stock separation. The harvest strategy of the Management Plan for the commercial sector of the Marine Scalefish Fishery will be reviewed in June 2018. This will involve developing more prescriptive reference points and decision rules and reconsideration of the management and monitoring boundaries based on the determination of stock structure from this project. As such, at that time, there will be opportunity to develop independent harvest strategies for the three stocks.

The SE regional population is part of the Western Victorian Stock that is reliant on variable recruitment into PPB, which drives the episodic nature of the regional population abundance, biomass and fishery productivity. As such, the future of this regional fishery depends on the stock status and fishery in PPB, which is managed by Fisheries Victoria. The recruitment index attained from annual 0+ sampling in PPB (Kemp et al. 2012), will inform a few years in advance of the likelihood of recruitment to the SE. Many of the fish that emigrate from PPB to the SE are likely to remain there and never return to re-join the spawning biomass in PPB, on which the Western Victorian Stock depends.

Historically, stock assessments for SA's snapper fishery have considered a number of regional populations that were recently assigned different levels of stock status, i.e. 'sustainable' for NGSV, 'transitional depleting' for each of NSG, SSG, SGSV and 'undefined' for the WC (Fowler et al. 2013). The current study has provided a biological basis for grouping these regional populations into two stocks, i.e. Spencer Gulf /West Coast (SG/WC) and Gulf St. Vincent (GSV).

Different harvest strategies could be applied to these two stocks to pursue different objectives, i.e. a strategy for conserving adult biomass could be implemented for the GSV stock, whilst one for rebuilding biomass could be applied for the SG/WC stock. Whilst introducing different strategies for managing the two stocks is tractable from a biological perspective, there remain complications such as the lack of zoning in the Marine Scalefish Fishery that could result in unwanted redistribution of fishing effort. As such, any process that involved applying different harvest strategies to different stocks would require significant consideration.

8. Extension and adoption

The need for this project became evident through the discussions of the Snapper Working Group (SWG) in 2011, and was supported by the Marine Fishers Association (MFA). Through the course of this study, progress reports have been provided to the Marine Scalefish Fishery Management Advisory Group, including a presentation of final results and conclusions that was given on 8 July 2015. Furthermore, preliminary results of the project were considered at two cross-jurisdictional meetings that involved fishery scientists, managers and fishing industry representatives from SA, Victoria and several other states. The first was a meeting of the National Snapper Steering Group held in Melbourne on 11 September 2014. The second presentation was given to the Western Victorian Stock Reference Group (WVSRG) on 12 September 2014, at which there was a particular focus on the western extent of the Western Victorian Stock. The final report will be made available to the MFA, WVSRG and PIRSA Fisheries and Aquaculture. The significant results of this project will soon feature in the on-going consideration of snapper management both at the intra-state and cross-jurisdictional levels.

Several presentations involving the results from this project have been given at national and international conferences by the Principal Investigator. These include a presentation at the Australian Society for Fish Biology (ASFB) & Oceania Chondrichthyan Society 2012 joint conference and symposium entitled 'Can spatial differences in the chronological structure of otoliths provide insight into the origins and large-scale movement of snapper (*Pagrus auratus*)?' Also, the presentation 'Analysis of phenotypic characteristics of otoliths – resolving stock structure issues for snapper in South Australia' was presented at the 5th International Otolith Symposium in October 2014. Two presentations were given at the annual meeting of the ASFB held in October 2015, i.e. 'Local movement behaviour of snapper (*Chrysophrys auratus*) through Northern Gulf St. Vincent, South Australia – determined through acoustic telemetry' and 'Otolith chemistry profiles for snapper (*Chrysophrys auratus*) – resolving issues of movement and stock structure'.

9. Recommendation

This project has significantly enhanced our understanding of the life history, demography, population dynamics and stock structure of snapper in south eastern Australia. It has confirmed the significance of recruitment variability as driving the broad-scale trends in fishery productivity, whilst also providing a better understanding of the spatial structure of the region. This spatial structure is divisible into three stocks, each of which depends on a significant nursery area. Furthermore, the regional populations that constitute each stock are replenished through emigration from its primary nursery area. From this understanding, it is now possible to consider any area of coastal waters of SA and western Victoria, and nominate the processes that led to the recent level of fishable biomass at that place. The temporal variation in local patterns of fishable biomass is driven by recruitment variability, subsequent migration, the time since the last strong year class and distance from the nursery area. Such understanding provides a strong base from which to facilitate the management of the fisheries on the different stocks. This means that uncertainty about the spatial scale at which fishery management should be considered has largely been resolved, which now allows stock assessment processes to be adapted to this more resolved spatial regime. This will require adaptation of the South Australian stock assessment computer model to the new spatial structure and may also involve changes in the model with respect to the emphasis on the different demographic processes.

9.1 Further development

This project has confirmed that the temporal dynamics in the fishable biomass of the various stocks is driven by inter-annual variability in recruitment for snapper. Understanding of this variability has proven elusive. It is likely that environmental factors that drive the variable recruitment dynamics differ between Port Phillip Bay and the two northern gulfs in SA. Nevertheless, identifying the different controlling processes would provide a basis from which to model and thereby predict the future trends in fishable biomass for the different stocks and their regional populations. Such modelling would be based on recruitment rates, subsequent emigration of fish from the nursery areas and their movement over the number of years following recruitment. This would allow planning with respect to gearing up or gearing down by fishers, as well as real-time management regimes to be implemented. As such, now that our understanding of the stock structure, the influence of variable recruitment and fish migration are better understood, it would be timely to concentrate research effort at the individual stocks to determine the causes of variable recruitment.

10. Appendices

10.1 Appendix 1. Project Staff

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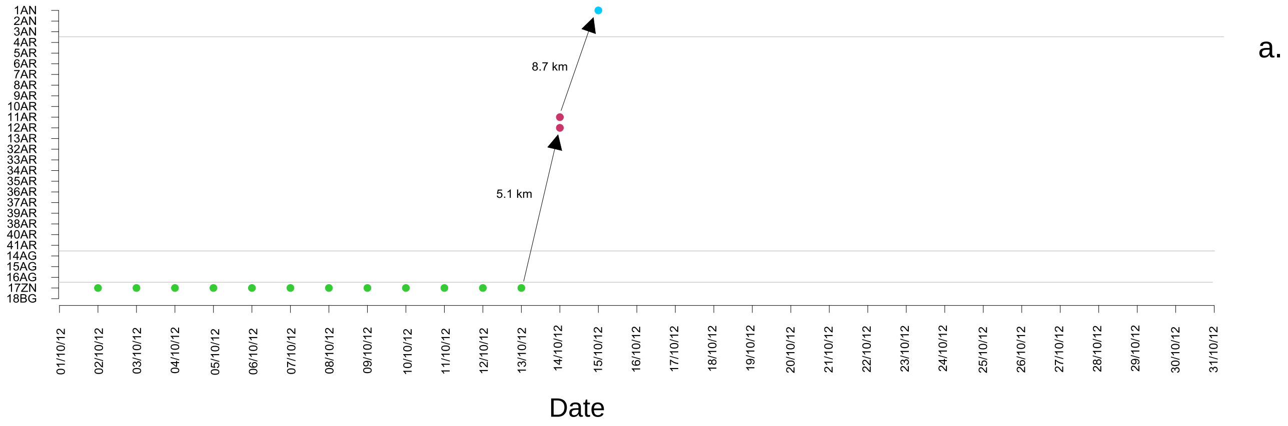
10.3 Appendix 3. Summaries of movement behaviour of individual fish

This appendix involves a series of figures that summarise the spatial and temporal aspects of the acoustic telemetry data for nine snapper considered in the acoustic telemetry study in NGSV. These figures augment those that were presented Chapter 5 to demonstrate the different types of space use and movement behaviour. The top figure for each fish shows the days on which the fish was recorded at each of the different listening stations for the duration of the fish's detection period. The bottom figure shows a map of the study area identifying a number of key stations at which the fish was detected. Furthermore, the temporal sequence of detections amongst the stations is indicated by arrowed lines. Note that these lines do not necessarily relate the direct movements of the fish but the directions of their displacement.



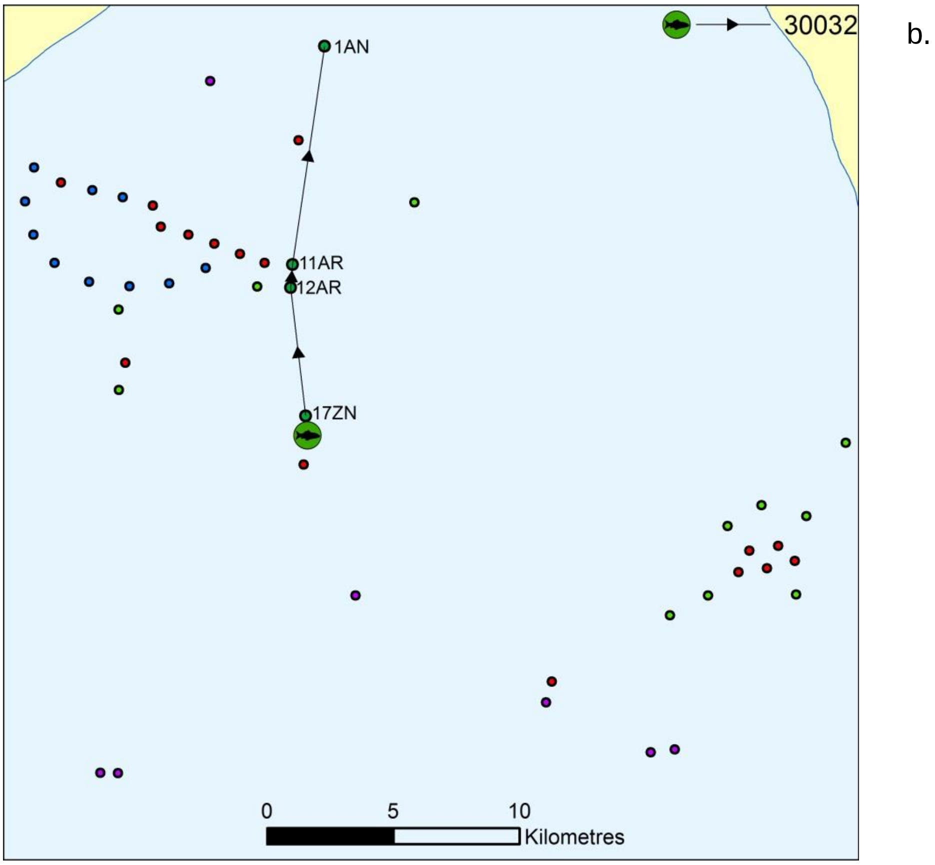


Fig. A11.1 Details of the movement behaviour of Fish 30032 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

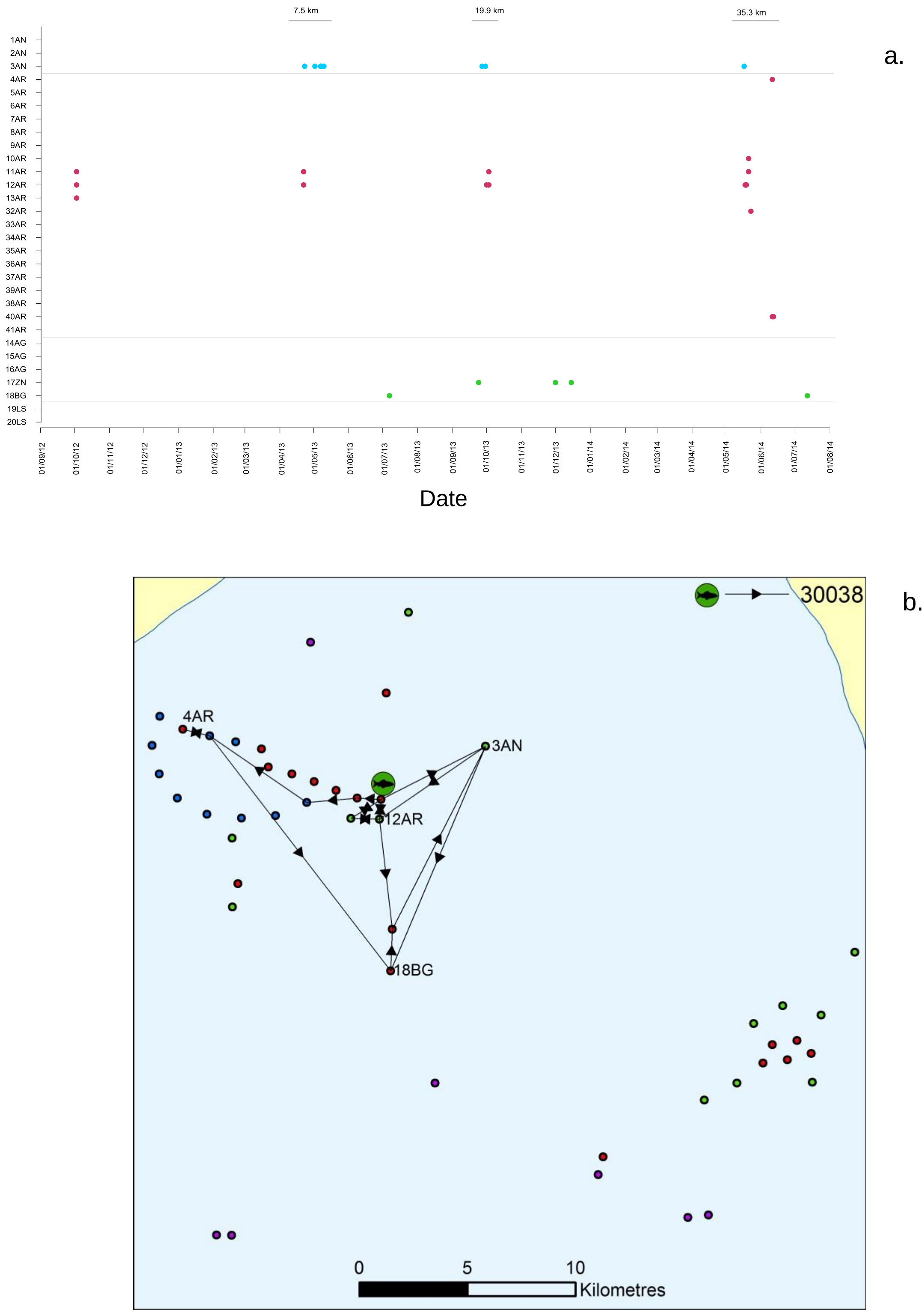
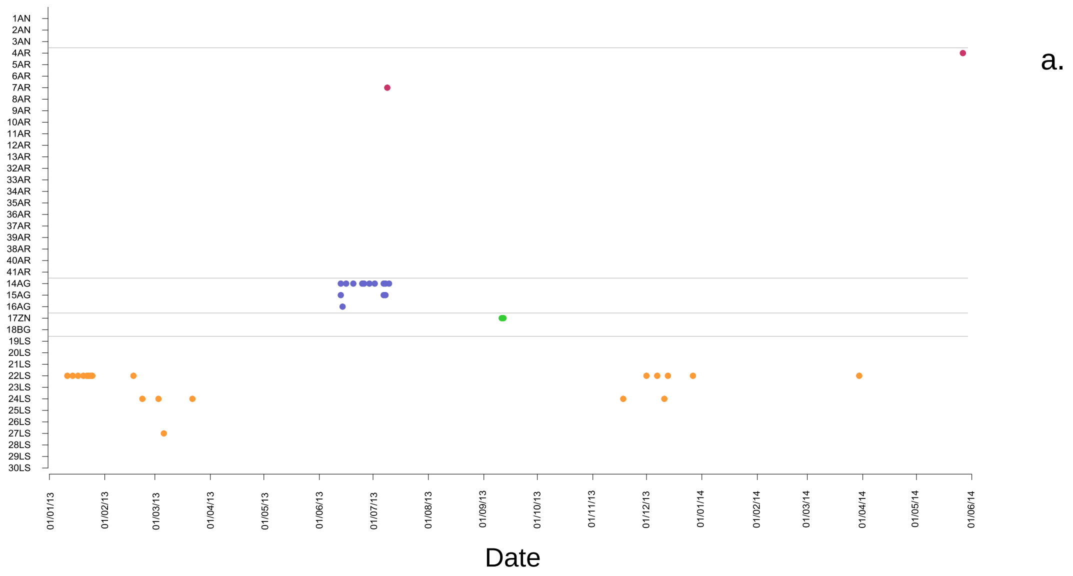


Fig. A11.2 Details of the movement behaviour of Fish 30038 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.



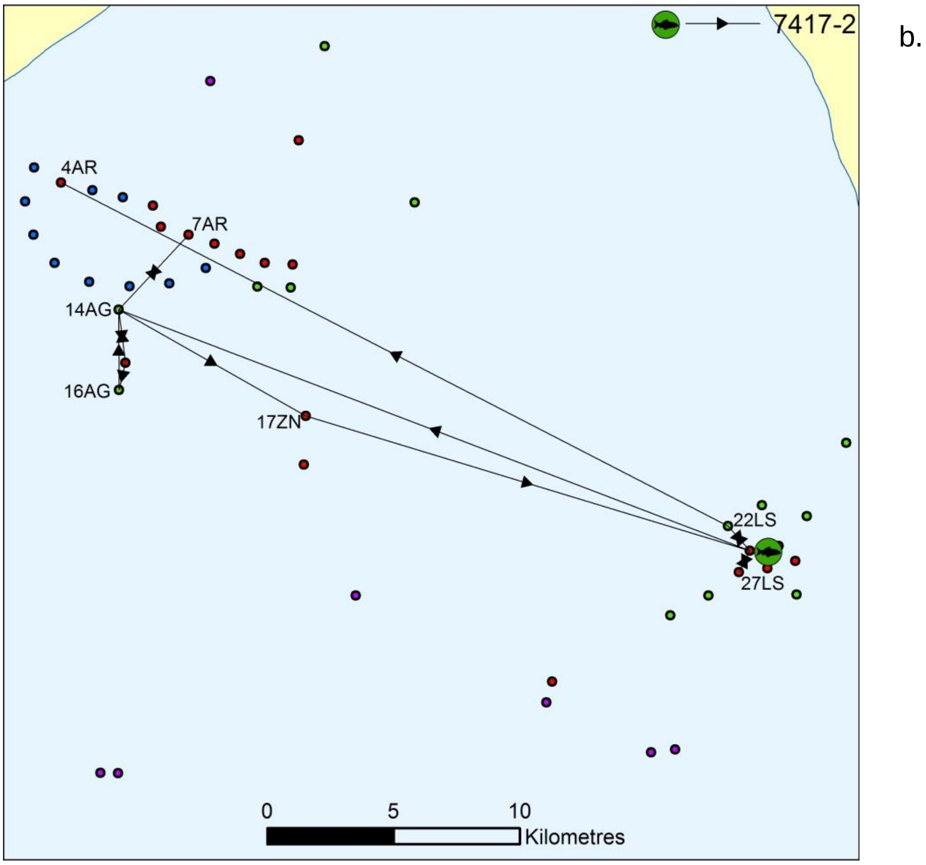


Fig. A11.3 Details of the movement behaviour of Fish 7417-2 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

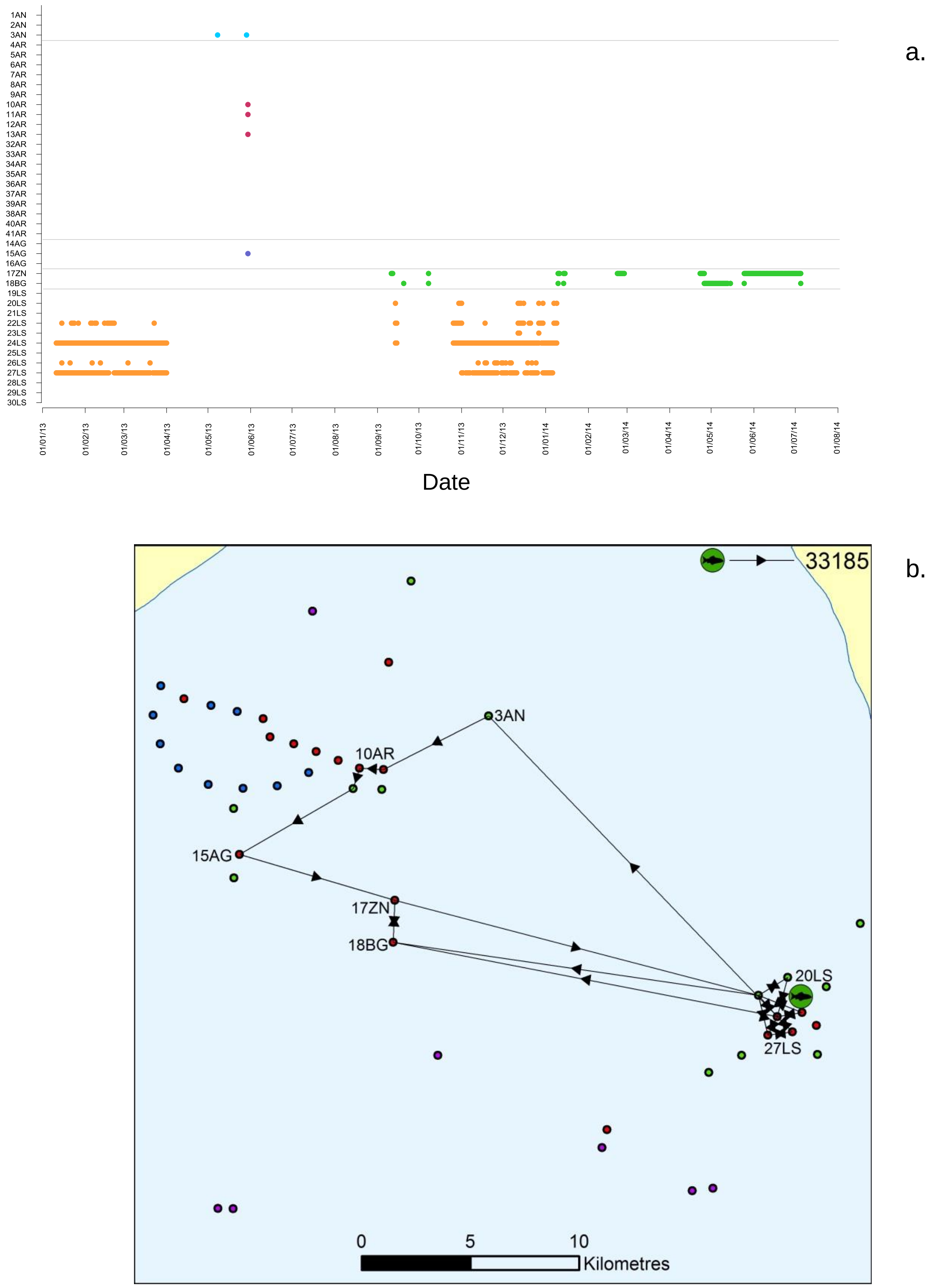


Fig. A11.4 Details of the movement behaviour of Fish 33185 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

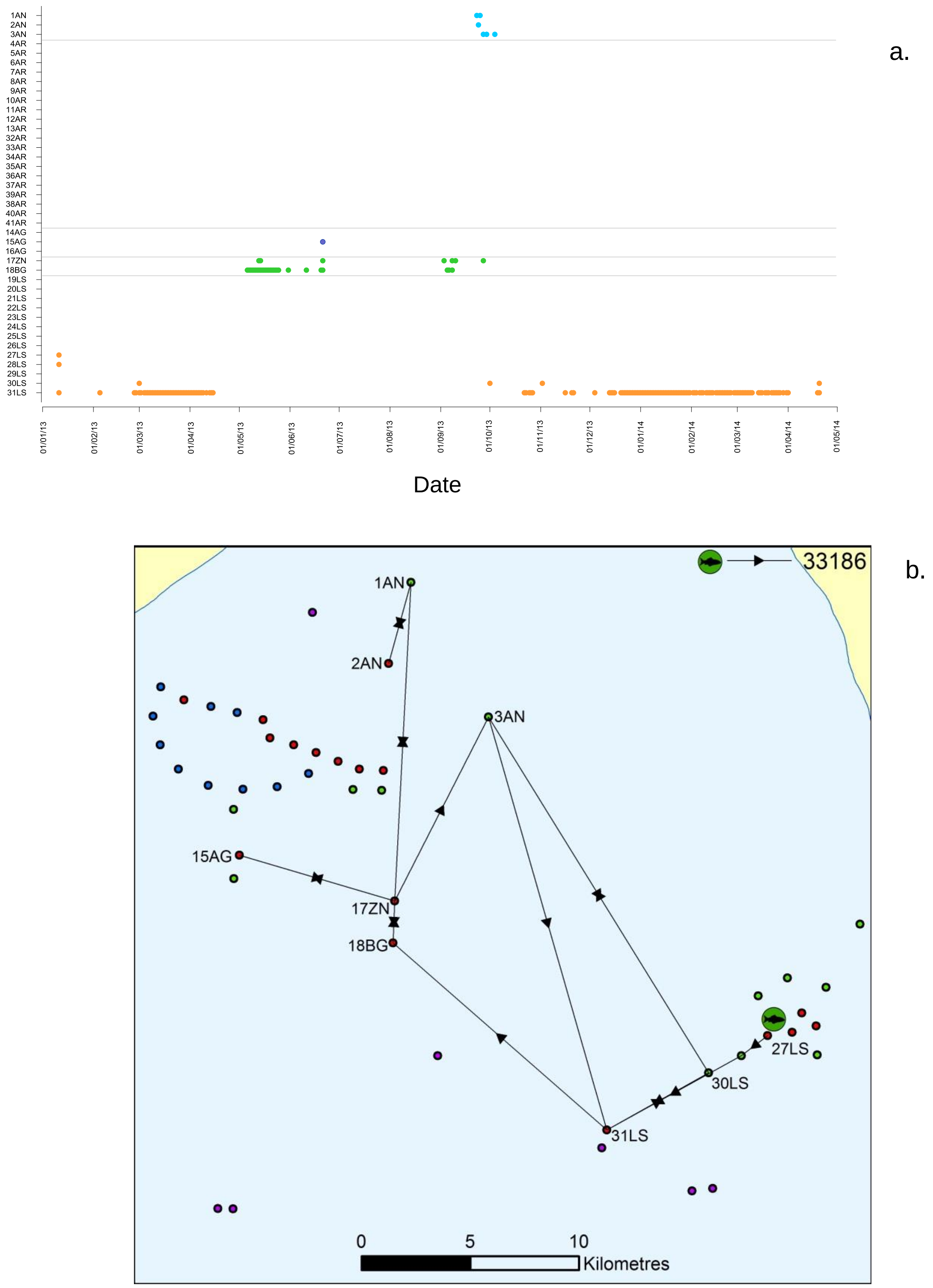
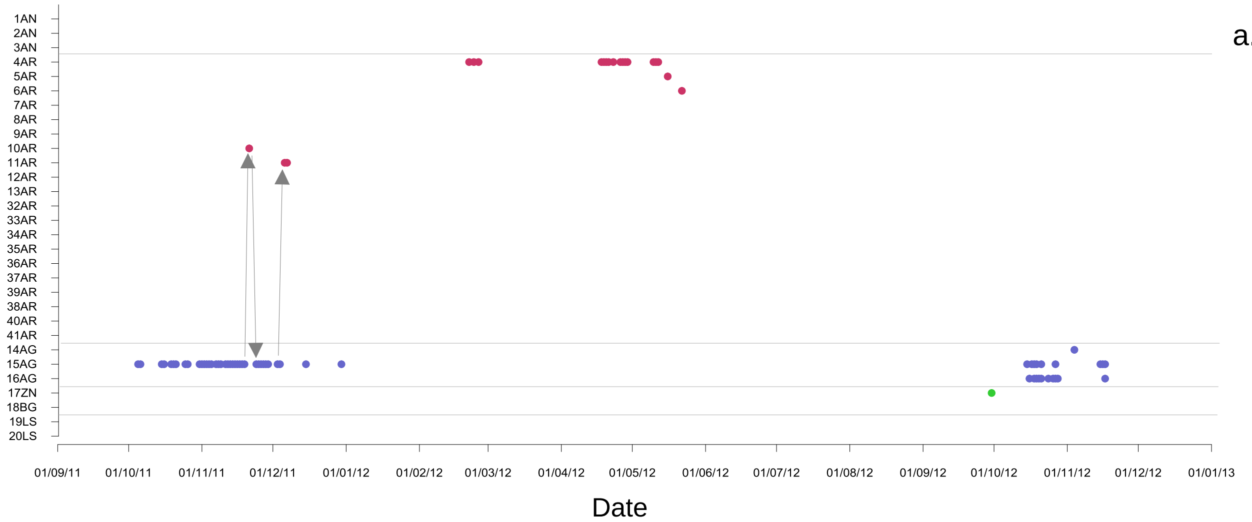
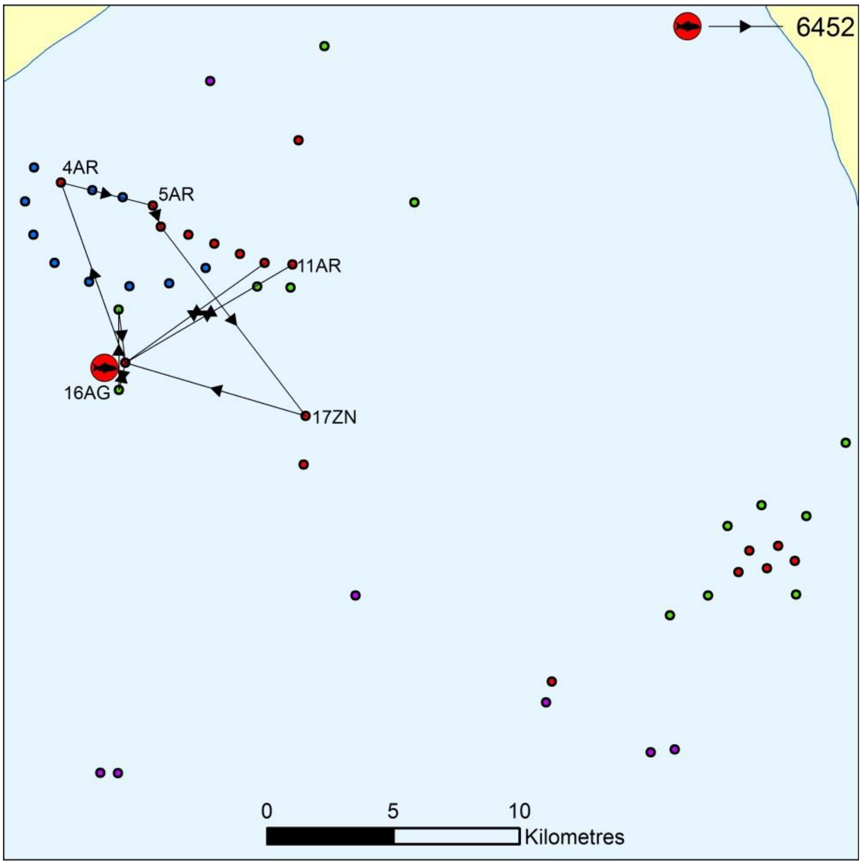


Fig. A11.5 Details of the movement behaviour of Fish 33186 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

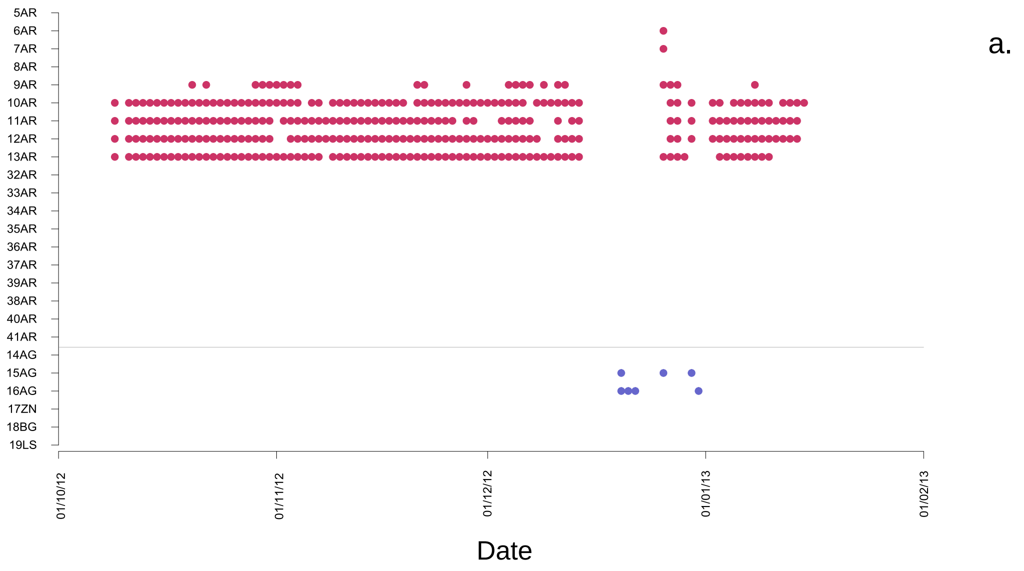


a.



b.

Fig. A11.6 Details of the movement behaviour of Fish 6452 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.



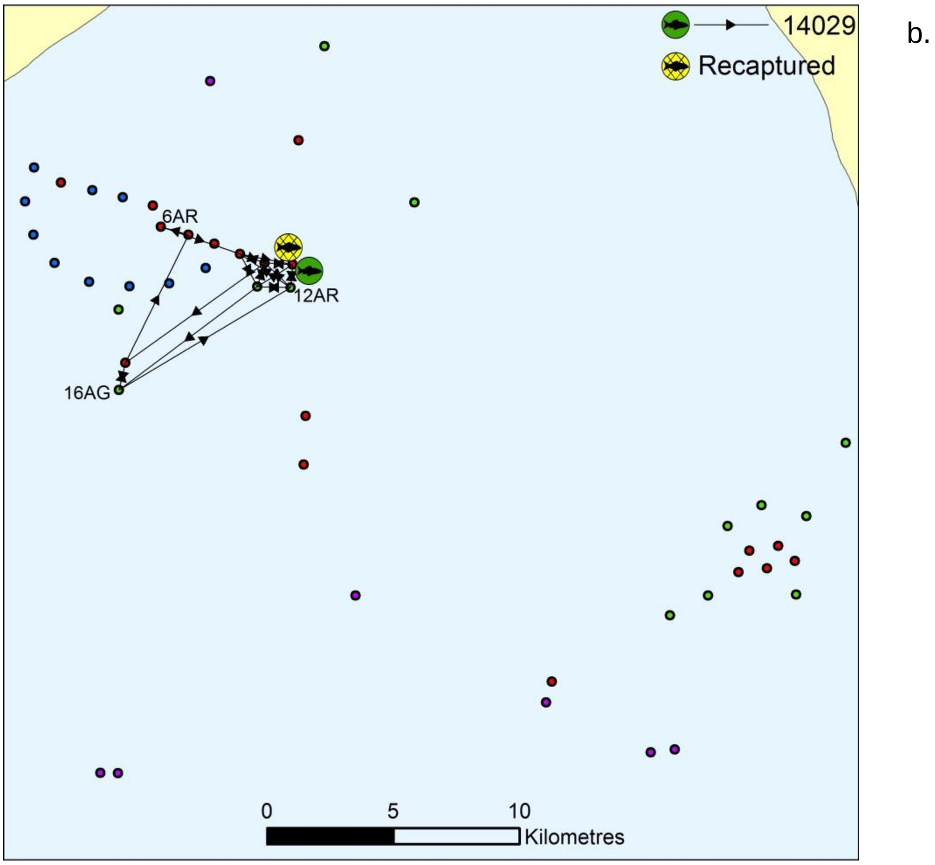


Fig. A11.7 Details of the movement behaviour of Fish 14029 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

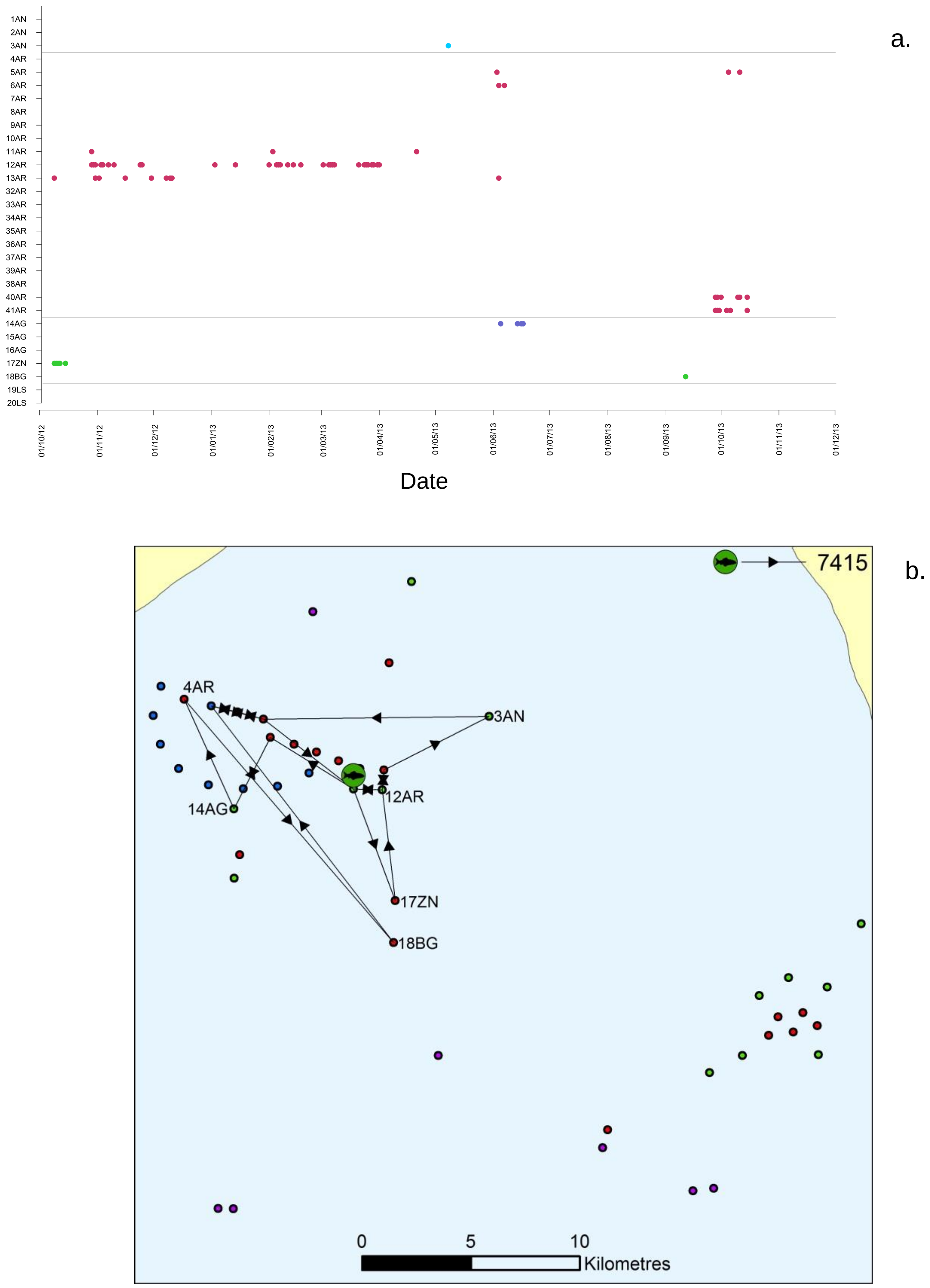


Fig. A11.8 Details of the movement behaviour of Fish 7415 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.

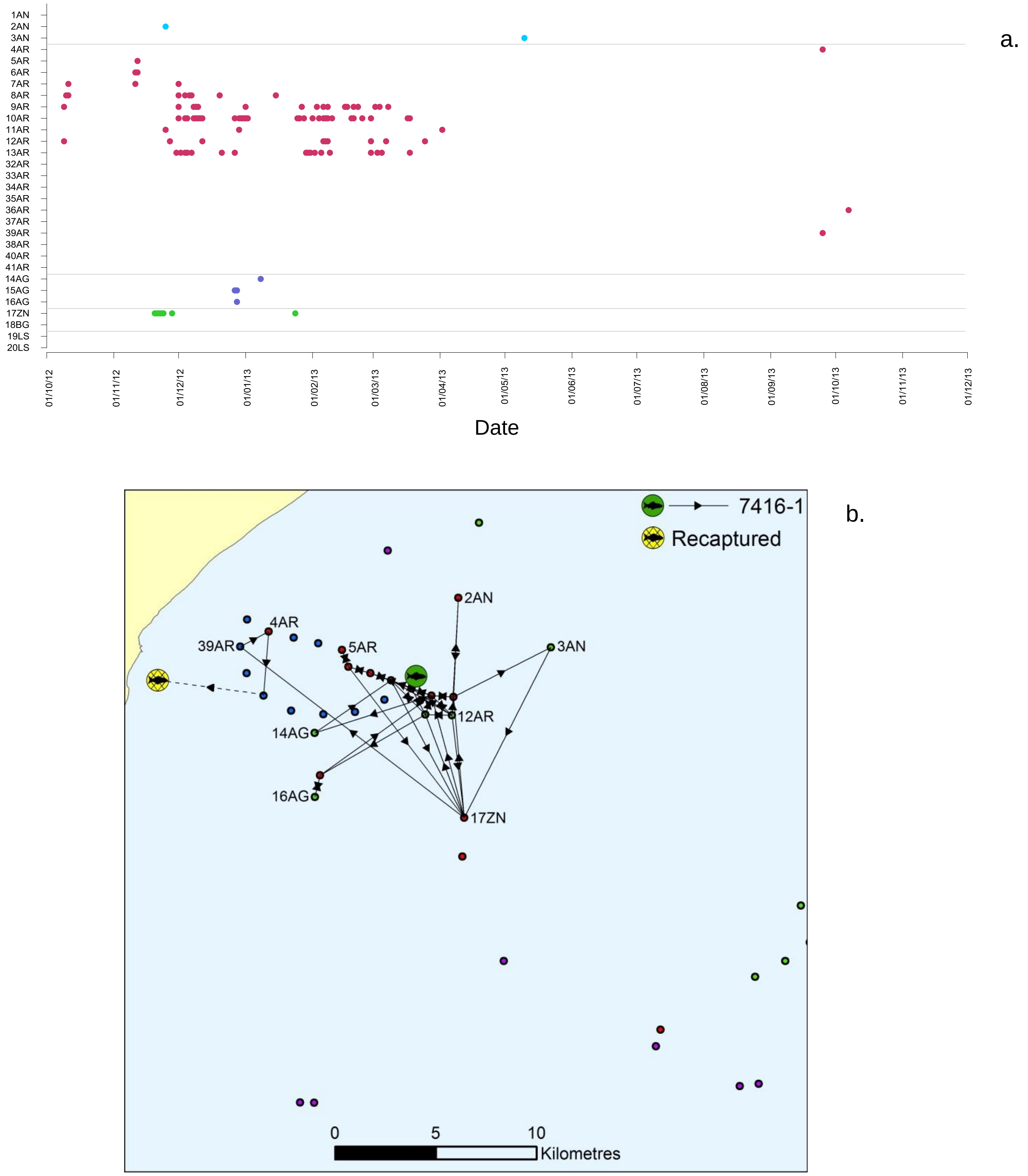


Fig. A11.9 Details of the movement behaviour of Fish 7416-1 from the acoustic telemetry study. a. daily detections at each nominated station. b. map of study area showing stations where detections were recorded. The temporal sequence of detections amongst stations is indicated by arrowed lines.