

The Life History and Stock Assessment of Anchovy, *Engraulis australis*, in South Australia.

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Table of Contents

TABLE OF CONTENTS	2
ABSTRACT	4
DECLARATION	6
ACKNOWLEDGEMENT:	7
GENERAL:	7
CHAPTER 2:	7
CHAPTER 3:	8
CHAPTER 4:	8
CHAPTER 1	9
INTRODUCTION	9
<i>Anchovy – General Background</i>	9
<i>Anchovy in Australia</i>	10
<i>Research</i>	11
<i>Thesis aims</i>	13
<i>Thesis chapters</i>	14
<i>Notes on chapter style</i>	17
CHAPTER 2	18
RELATIVE IMPORTANCE OF GULF AND SHELF WATERS FOR SPAWNING AND RECRUITMENT OF AUSTRALIAN ANCHOVY, <i>ENGRAULIS AUSTRALIS</i> , IN SOUTH AUSTRALIA	18
<i>Statement of Authorship</i>	19
<i>Abstract</i>	20
<i>Introduction</i>	20
<i>Methods</i>	24
Spawning season	24
Ichthyoplankton surveys	24
Gonosomatic index	24
Gulf and shelf oceanographic surveys	25
Egg and larval distributions in gulf and shelf waters	26
a. Spawning distribution	26
b. Anchovy larvae size-class distribution	27
<i>Results</i>	27
Spawning season	27
Gulf and shelf oceanographic surveys	28
Egg and larval distribution in gulf and shelf waters	32
a. Spawning distribution	32
Anchovies	32
Sardines	34
b. Anchovy larvae size-class distributions	35
<i>Discussion</i>	38
CHAPTER 3	43
AGE-STRUCTURED REPRODUCTIVE STRATEGY OF AUSTRALIAN ANCHOVY (<i>ENGRAULIS AUSTRALIS</i>) DETERMINED BY OTOLITH MICROSTRUCTURE ANALYSIS	43
<i>Statement of Authorship</i>	44
<i>Abstract</i>	45
<i>Introduction</i>	45

<i>Materials and methods</i>	49
Sampling	49
Historical data.....	50
Otolith analysis - adults	51
Length-based analysis.....	52
Length at maturity	52
<i>Results</i>	53
Length-frequency	53
Regional length/frequency comparisons.....	56
Age and Growth Rates	57
Length at maturity	59
<i>Discussion</i>	60
CHAPTER 4	64
SPAWNING DYNAMICS AND BIOMASS ESTIMATES OF AN ANCHOVY (ENGRAULIS AUSTRALIS) POPULATION IN CONTRASTING GULF AND SHELF ENVIRONMENTS.	64
<i>Statement of Authorship</i>	65
<i>Abstract</i>	66
<i>Introduction</i>	66
<i>Methods</i>	69
<i>Results</i>	77
<i>Discussion</i>	81
CHAPTER 5	87
GENERAL DISCUSSION	87
CONCLUSIONS.....	93
FUTURE RESEARCH.....	95
APPENDIX A – TITLE PAGE REPRINTS	97
APPENDIX B – COPYRIGHT PERMISSIONS	100
BIBLIOGRAPHY	105

Abstract

The abundance and distribution of small pelagic fish in coastal upwelling systems fluctuate in response to environmental or biotic factors acting on larval stages. Anchovies (*Engraulis spp.*) have evolved flexible adaptive strategies to maximise recruitment in such environments. Spawning usually occurs throughout coastal and shelf regions, however the relative importance of inshore/offshore waters for spawning and the survival of eggs and larvae is poorly understood.

The objectives of this study were to 1-identify the locations, and season, of anchovy (*Engraulis australis*) spawning in South Australia; 2-determine the oceanographic and biotic characteristics (e.g sea-surface temperature and chlorophyll *a* levels,) of gulf and shelf waters during the spawning season of this species, and 3-determine the relative importance of gulf and shelf waters for anchovy spawning and larval recruitment.

Ichthyoplankton and oceanographic surveys encompassing a total of 128,700 km² were conducted and anchovies were captured at locations throughout this area. Anchovy eggs were found throughout gulf and shelf waters, with highest densities recorded in northern areas of Spencer Gulf and Gulf St Vincent where sea surface temperatures (SST) were 24–26°C. Spawning appeared to peak between 0000 and 0100 hours.

Otolith increment counts were used to age larval, juvenile and adult anchovies from both shelf and gulf waters. In the northern Spencer Gulf only smaller, young fish up to 1 year of age occurred, where there were eggs and young larvae (< 10 mm) at high density. These anchovies spawned relatively small batches of eggs (c. 855 per fish) approximately every 3 days over an area of approximately 4,898 km². The daily egg production method (DEPM), used to estimate an adult biomass for the northern Spencer Gulf gave an estimate of 25,374 tonnes.

The southern gulf area was inhabited by 1, 2 and 3 year old fish, whereas over the continental shelf, where upwelling occurs, 3, 4, and 5 year old fish were found. In these cooler, deeper, shelf waters, where the larger, older, anchovies are found, lower egg densities occurred despite individuals producing much larger batches of eggs (ca.

15,572 per fish) approximately every 7 days. In shelf waters, the highest egg densities were recorded at inshore sampling stations. Spawning by older fish took place over a far greater area of ca. 44,618 km² with an estimated adult biomass of 101,522 tonnes. Unlike in the gulf waters, larvae > 10 mm total length (TL) were mainly found with the largest larvae, > 15 mm TL, being collected from shelf waters near up-welling zones where SSTs were relatively low (< 20°C) and levels of chlorophyll a (chl *a*) relatively high. The high levels of larval abundance in the upwelling zones may reflect higher levels of recruitment to later stages in these areas compared with the gulfs.

Gonosomatic indices, together with egg and larval densities, indicated that the peak spawning season was from January to March. This coincided with the enhanced period of productivity in shelf waters due to up-welling events. However, these highly variable environments can be highly dispersive with resulting high egg and larval mortalities and are generally dominated by sardines (*Sardinops spp.*). In addition to the shelf population young fish are also present in the relatively stable gulf environment. This population may act as a reserve of anchovy in South Australia from which the population may expand under favourable conditions. When the population of dominant sardines (*S. sagax*) are reduced, it appears that the subordinate anchovies, represented by older age-classes, are able to utilise offshore environments which may then provide additional spawning and nursery areas for this species.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution to Wetjens Dimmlich and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968. The author acknowledges that copyright of published works contained within this thesis (as listed below) resides with the copyright holder(s) of those works.

1. Dimmlich, W. F., Breed, W. G., Geddes, M. & Ward, T. M. (2004). Relative importance of gulf and shelf waters for spawning and recruitment of Australian anchovy, *Engraulis australis*, in South Australia. *Fisheries Oceanography* **13**, 1-14.

<http://www3.interscience.wiley.com/journal/118799314/abstract>

2. Dimmlich, W. F. & Ward, T. M. (2006). Ontogenetic shifts in the distribution and reproductive patterns of Australian anchovy (*Engraulis australis*) determined by otolith microstructure analysis. *Marine and Freshwater Research* **57**, 373-381.

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3. Dimmlich, W. F., Ward, T. M. & Breed, W. G. (2009). Spawning dynamics and biomass estimates of an anchovy, *Engraulis australis*, population in contrasting gulf and shelf environments. *Journal of Fish Biology* **75**, 1560-1576.

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November 25, 2010.

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skipper, Neil Chigwidden, and crew, Chris Small, Dave Kerr and Ralf Putz, of the *R.V. Ngerin* were crucial to the successful completion of the research cruises. The research and preparation of this manuscript was jointly supported and funded by the South Australian Research and Development Institute (Aquatic Sciences) and a University of Adelaide PhD scholarship.

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Chapter 1

INTRODUCTION

Anchovy – General Background.

Small pelagic fishes are important components of many up-welling marine ecosystems where they facilitate the transfer of energy from lower to higher trophic levels (Cury *et al.* 2000). Their life histories, which are characterised by short life spans and rapid growth, in conjunction with highly variable recruitment, are a product of the dynamic environments in which they spawn. Many fisheries investigations have been able to establish significant correlation of pelagic fish species abundance to such factors as temperature fronts and eddies, depth of the thermocline, primary and secondary production and bottom topography-current interactions (eg. Bakun 2006a; Swartzman *et al.* 1994).

Anchovies (*Clupeoides*; *Engraulidae*; *Engraulis*) are typical of many small pelagic fishes. They are relatively short-lived (~7 years), schooling, planktivorous, batch-spawning, fish that inhabit mainly shallow, coastal waters and estuaries in both tropical and temperate regions. They form dense populations and support large fisheries in upwelling areas, such as those found along the west coast of Peru and southern Africa.

Anchovy spawning patterns can vary in response to a range of environmental factors (Nelson *et al.* 1994; Castillo *et al.* 1996; Cole and McGlade, 1998; Castro *et al.* 2000; Kim and Lo, 2001; Ward *et al.* 2003) with the peak spawning period often occurring during warmer months and/or during periods of enhanced productivity by offshore seasonal oceanographic processes (Roy *et al.* 1989; Nelson *et al.* 1994; Borja *et al.* 1998; Aoki and Miyashita, 2000). However, some studies have suggested that rates of larval survival are higher in some inshore than offshore areas (Brewer and Smith, 1982; Hewitt and Brewer, 1983; Castro *et al.* 2000).

Previous studies suggest that anchovies have evolved a flexible reproductive strategy so

that recruitment can be maximised in such variable environments (Shelton and Hutchings 1981; Palomera 1992; Hugget *et al.* 2003; Wilhelm *et al.* 2005) with different components of the adult population spawning in different regions (Owen *et al.* 1989). Studies of age and growth of anchovies undertaken in other ecosystems have produced some evidence to support these ideas (e.g. Melo 1984; Bellido *et al.* 2000; Cuttita *et al.* 2003; Basilone *et al.* 2004).

The spawning seasons, spawning grounds and juvenile nursery areas of anchovy often overlap those of sardine (*Sardinops spp.*) (Schwartzlose *et al.* 1999; Smith *et al.* 2001; Ward and Staunton-Smith, 2002) with fluctuations in the relative abundance of sardines and anchovies observed in many ecosystems (Schwartzlose *et al.* 1999; Nakata *et al.* 2000).

Anchovy in Australia

The Australian anchovy (*Engraulis australis*) is the only engraulid endemic to southern Australia and is found throughout temperate coastal waters where spawning takes place during summer and autumn (Arnott and McKinnon, 1985; Jenkins, 1986; Fletcher and Tregonning, 1992; Hoedt and Dimmlich, 1995). In contrast to the majority of engraulids, *E. australis* is found in, what was believed to be, relatively low productivity waters with stocks thought to be generally small (Kailola *et al.* 1993). Both the shelf and gulf regions of South Australia are occupied by components of the anchovy population. These are, however, very different environments which are separated during summer by thermal and saline frontal systems at the entrance to the gulfs (Bruce & Short, 1990). This combined region is unique within the Australian context as productivity is enhanced over the shelf by annual up-welling of cool nutrient-rich water (Kampf *et al.* 2004; McClatchie *et al.* 2006; Ward *et al.* 2006) whereas the warm waters of the gulfs lack sources of nutrient enrichment with the consequence that their primary and secondary production is low.

Although anchovies are one of the best understood fish families in the world, in Australia they have not been the subject of extensive investigations with few data available on most aspects of their biology. In South Australia, virtually no information

has been available until recently for the anchovy, although there is increasing evidence of the species' importance within the South Australian marine ecosystems (Ward *et al.* 2008, McLeay *et al.* 2009; Wiebkin, pers. comm.). The South Australian marine ecosystem is similar to many which feature numerous species at the lower and upper trophic levels, but are constricted at the mid trophic level to one or several dominant planktivorous forage-fish species. These systems have been referred to as “wasp-waist” ecosystems (Rice 1995; Bakun 2006b; Cury *et al.* 2000).

To date, only minor anchovy fisheries have been established in Australia, mainly in Victoria (Blackburn 1950; Hobday 1992; Ward *et al.* 1998). Historically, few anchovies have been harvested in South Australia, and no biological data have yet been published on the population of this species in this state. Relatively few ageing studies have been attempted in Australia with no information available for South Australia on the age structure of the spawning anchovy populations in the two environmentally distinct shelf and gulf regions. However, the establishment in the mid-1990's of a purse seine fishery in South Australia targeting sardines (*Sardinops sagax*) (including an unquantified anchovy bycatch) and an increased demand for small pelagic fishes throughout Australia, has led to the recent development of an experimental fishery for *E. australis* in this state and thus the need for additional baseline data to increase understanding and support management of the species.

Research in Australia

The high economic value of anchovies elsewhere has led to the development and application of a large range of sophisticated biological studies and stock assessment techniques to determine stock abundance of a number of anchovy populations including those of the northern anchovy (*E. mordax*), Peruvian anchovy (*E. ringens*), southern Benguela and European anchovy (*E. encrasilocus*) (Bindman, 1986; Cubillos *et al.* 2007; Shelton *et al.* 1993; Motos & Santiago, 1990; Palomera & Pertierra, 1993). The most commonly used methodology has involved the daily egg production method (DEPM; Lasker 1985) which operates under the premise that spawning biomass can be calculated from estimates of the numbers of eggs produced per day in the spawning

area (daily egg production) and the number of eggs produced per unit mass of population (daily fecundity).

The parameters required for inclusion into the ichthyoplankton-based DEPM of estimating spawning biomass are the spawning area, daily egg production, average female weight, batch fecundity, spawning fraction and sex ratio. These requirements have resulted in extensive associated investigations into the ecology and biology of anchovies. Large variations in batch fecundity within single clupeoid populations have been reported (Alheit 1989; Alheit 1988; Tsurita & Hirose 1989; Luo & Musick 1991) and have been attributed to fluctuations in ambient water temperatures and productivity (Funamoto & Aoki, 2002; Somarakis *et al.* 2002; Takasuka *et al.* 2005; Stratoudakis *et al.* 2007), levels of fat reserves stored during lead-up periods to spawning (Hunter & Leong 1981) and food availability during the spawning season (Tsuruta & Hirose 1989). Increases in batch fecundity in relation to size of the northern anchovy (*E. mordax*) have been identified with up to a tenfold increase in annual egg outputs by a female between her first and fourth spawning seasons (Parrish *et al.* 1986). These effects have prompted recommendations for further inshore-offshore comparison of the spawning ecology of small pelagic fish subject to DEP methodologies in order to improve the effectiveness of this methodology in estimating overall biomass (Takasuka *et al.* 2005).

In contrast to elsewhere, anchovy research in Australia has been very limited. The effect of hydrographic parameters on egg distribution in the Gippsland Lakes, Victoria, was investigated by Arnott and McKinnon (1985) and seasonal egg and larval distributions around Phillip Island, Victoria, were examined by Hoedt and Dimmlich (1995) and Hoedt *et al.* (1995). Spawning patterns of anchovy in relation to other small pelagic species including the sardine (*Sardinops sagax*) in south-eastern Queensland have also been investigated (Ward *et al.* 2003).

No recent studies of age and growth of *E. australis* have been attempted since growth increments in scales were used in early aging studies (e.g. Blackburn 1950) but this method of age determination has declined in favour of otolith-based methods in recent

years after several studies (Pertierra and Morales-Nin 1989; Francis *et al.* 1992; McFarlane and Beamish 1995) showed that scale-based approaches may underestimate the ages of clupeids and other fish species.

In South Australia the distribution of anchovy is known to be widespread over shelf waters, but relatively little information is available on its distribution and abundance in the northern parts of the two large gulfs which characterise the South Australian coastline, the Spencer Gulf and Gulf St Vincent, where significant assemblages of *E. australis* larvae had been reported (Ward *et al.* 2000).

Thesis aims

The aims of this thesis were to:

- obtain estimates of population parameters for *E. australis* in South Australia, including geographic range;
- determine the timing, frequency and location of spawning, patterns of ageing for *E. australis* in South Australia;
- determine the stock size of *E. australis* in both the gulf and shelf waters (both largely unfished engraulid stocks) through the application of biological and stock assessment techniques developed for other engraulids.

This research has been conducted within the broader framework of a study designed to compare the life history of an engraulid from, what is believed to be, a relatively low productivity region with patterns observed for similar species in known high productivity regions. Several questions of primary interest for *E. australis* in South Australian waters were identified. These were:

1. What is the distribution and abundance of *E. australis* eggs and larvae
2. What environmental factors influence the distribution and abundance of *E. australis* eggs and larvae? Hypothesis to be tested is:

- a. That egg and larvae abundance are correlated with water temperature, and/or zooplankton abundance and/or chlorophyll levels.
3. What are the growth patterns of this species? Hypotheses to be investigated:
 - a. That microstructures within *E. australis* otoliths represent daily and annual events in the anchovy life-cycle.
 - b. Growth rates are lower than those of other engraulid species.
 4. What is the population density/size? Hypotheses to be investigated:
 - a. Density of anchovy eggs and larvae in South Australian waters is relatively low in comparison to those observed for other engraulids species in high productivity regions.
 - b. There is a relatively small stock of *E. australis* in South Australia.

Thesis chapters

Chapter Two. This presents the results of ichthyoplankton surveys carried out over two summer spawning seasons during 2000 and 2001 for the current study. Surveys were carried out throughout shelf waters and incorporated a comprehensive investigation of the northern gulf regions with eggs and larvae collected at all sampling stations. The surveys conducted in the gulfs were carried out by outboard motor vessel able to operate in the shallower waters and the offshore surveys were carried out using the South Australian Research and Development Institute's *RV Ngerin*.

To supplement the results of the 2000-2001 surveys, archived zooplankton samples obtained during a series of research cruises conducted from 1986 to 1999, unrelated to the current study, were sorted and anchovy eggs and larvae extracted. The data from the current study, together with the supplementary data from archived samples were amalgamated into a single comprehensive dataset assumed to be representative of the spatial and temporal distribution of *E. australis* during the spawning season throughout South Australia. This enabled the regional distribution and abundance of the species to

be determined in addition to identifying the locations and season of anchovy spawning.

The results of the ichthyoplankton surveys, combined with additional abiotic and biotic data collected during the field sampling programme facilitated an examination of the oceanographic and biotic characteristics of both shelf and gulf waters during the spawning season and provided information on the possible causal effects for larval survival after spawning in both shelf or gulf waters. Chlorophyll *a* estimates were used as proxies for primary production data with the assumption that differences in chlorophyll concentration between areas observed also indicated differences in primary production (Patti *et al.* 2010). Possible positive relationships between anchovy egg and larval density and the prevailing environmental conditions such as water temperature, zooplankton abundance, and/or chlorophyll levels were determined. A gonosomatic index for anchovy in South Australia was also established using data from adult fish sampled from 2000-2001.

Finally, possible interspecific interactions between anchovy and sardine were also investigated using data on sardine eggs and larvae collected during the ichthyoplankton surveys.

Chapter Three. This presents the results of the study of age and growth of anchovy throughout South Australian waters. Data used in this chapter were obtained from sampling of juvenile and adult anchovies throughout shelf and gulf waters from 2000-2001. Estimates of ages and growth rates were obtained for larval, juvenile and adult anchovies using both increment analysis and length-based methods. The use of direct counts of otolith microincrements (rings laid down in otoliths which are thought to exhibit a daily or annual periodicity) was the primary age determination technique used in the current study.

Age estimates provided by length-based methods have also been used to independently corroborate the timing of increment formation in otoliths (Campana 2001). These were also used in the current study.

This information, from both otolith- and length-based methods, were used to compare

the age and size structures of samples of anchovies obtained from northern Spencer Gulf, southern Spencer Gulf and shelf waters. Finally, the sizes-at-age of anchovies from these regions were compared with results reported in earlier studies carried out in similar environments elsewhere (Blackburn 1950; Hobday 1992; Hoedt and Dimmlich 1995).

Chapter Four. This chapter includes a biomass assessment of the anchovy, together with an independent assessment of the separate spawning populations in the shelf and gulf regions of South Australia.

For the biomass estimates, the data used were obtained from ichthyoplankton and juvenile and adult sampling conducted during the 2000 spawning season, throughout the geographic range of anchovy in South Australian waters (identified in Chapter Two). This was achieved by extending ichthyoplankton surveys in 2000 to the northern gulfs in order to obtain samples of both adult anchovies and eggs. The daily egg production model (DEPM) was used to provide the biomass estimates. For this the mean female weight, sex ratio, fecundity and spawning fraction and abundances of anchovy eggs was used to calculate the daily rate of size-specific egg production for both the gulf and shelf waters.

Data obtained through egg and larval sampling (Chapter Two) were used to determine egg and larval densities (m^{-3}) which were then compared to published density estimates obtained from other engraulid species worldwide. These data, in addition to information collected in other components of this study, were then used to determine spawning stock size through implementation of the daily egg production method (DEPM; Lasker 1985)

However, the apparent stratification by age of the anchovy spawning areas in South Australia identified by the current study (Chapter Three) presented further considerations. Within the South Australian population of spawning adults, parameters used in the application of the DEPM were likely to differ significantly between the smaller fish found in the northern gulfs and the larger fish occurring offshore in shelf

waters. It is suggested that would more robust application of the DEPM should take into account such variations within different components of a single population.

Chapter Five. This chapter concludes the thesis by synthesising the information from the preceding chapters and suggests some directions for future research on the anchovy in South Australia.

Notes on chapter style

Each of Chapters 2 - 4 incorporates the final pre-publication drafts of papers that were submitted and have been accepted for publication by the journals in which each paper has appeared. These papers can be read as individual stand-alone entities. However the papers in this thesis are presented in a logical progression of ideas, each chapter /paper building on the findings of the former chapter/paper to form a comprehensive investigation of the life history, biology and stock assessment of the anchovy in South Australia. Figures and Tables used in the papers have been renumbered to conform to chapter numbering in the thesis.

The Appendix presents the original title pages of the published manuscripts. Reprints of these final, published, papers are available on request from the author.

References have been consolidated in a single Bibliography.

Chapter 2

RELATIVE IMPORTANCE OF GULF AND SHELF WATERS FOR SPAWNING AND RECRUITMENT OF AUSTRALIAN ANCHOVY, *ENGRAULIS AUSTRALIS*, IN SOUTH AUSTRALIA

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Fisheries Oceanography, 2004: 13, pp. 310-323

Statement of Authorship

Relative importance of gulf and shelf waters for spawning and recruitment of Australian anchovy, *Engraulis australis*, in South Australia. **Fisheries Oceanography, 2004: 13, pp. 310-323**

DIMMLICH, W.F. (Candidate)

Conducted fieldwork, performed analysis on all samples, interpreted data, primary and corresponding author of paper.

I hereby certify that the statement of contribution is accurate

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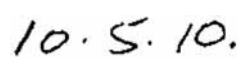
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Abstract

Gonosomatic indices and egg and larval densities observed from 1986 to 2001 suggest that the peak spawning season of the Australian anchovy (*Engraulis australis*) in South Australia occurs during January to March (summer and autumn). This coincides with the spawning season of sardine (*Sardinops sagax*) and the period when productivity in shelf waters is enhanced by upwelling. Anchovy eggs were abundant throughout gulf and shelf waters, but the highest densities occurred in the northern parts of Spencer Gulf and Gulf St Vincent where sea surface temperatures (SST) were 24°C-26°C. In contrast, larvae >10 mm total length (TL) were found mainly in shelf waters near upwelling zones where SSTs were relatively low (<20°C) and levels of chlorophyll-*a* (chl *a*) relatively high. Larvae >15 mm TL were collected only from shelf waters near upwelling zones. The high levels of larval abundance in the upwelling zones may reflect higher levels of recruitment to later stages in these areas compared with the gulfs. The sardine spawns mainly in shelf waters; few eggs and no larvae were collected from the northern gulfs. The abundance of anchovy eggs and larvae in shelf waters increased when sardine abundance was reduced by large-scale mortality events, and decreased as the sardine numbers subsequently recovered. We hypothesise that the upwelling zones provide optimal conditions for the survival of larval anchovy in South Australia, but that anchovy can only utilise these zones effectively when the sardine population is low. At other times, northern gulf waters of South Australia may provide a refuge for the anchovy that the sardine cannot utilise.

Key words: anchovy (*Engraulis australis*), clupeoid, eggs, inshore–offshore distribution, larvae, sardine (*Sardinops sagax*), spawning, upwelling

Introduction

Anchovies (*Engraulis spp.*) inhabit inshore and continental shelf waters of temperate and subtropical regions. Their spawning patterns vary in response to a range of environmental factors (Castillo *et al.* 1996; Castro *et al.* 2000; Kim and Lo, 2001; Ward *et al.* 2003) with the peak spawning period often occurring during warmer months and/or periods when productivity is enhanced by seasonal oceanographic processes

(Roy *et al.* 1989; Nelson *et al.* 1994; Borja *et al.* 1998; Aoki and Miyashita, 2000). Spawning usually occurs throughout coastal and shelf waters (Brewer and Smith, 1982; Fletcher and Tregonning, 1992; Beckley and Hewitson, 1994; Hoedt and Dimmlich, 1995), however the relative importance of inshore/offshore waters for spawning and the survival of eggs and larvae is poorly understood.

Significant differences in the levels of anchovy spawning activity in inshore and offshore waters have not been identified, but some studies have suggested that rates of larval survival are higher in some inshore areas (Brewer and Smith, 1982; Hewitt and Brewer, 1983; Castro *et al.* 2000). In the eastern and western boundary current systems, the key spawning areas usually coincide with the main larval nursery areas (Hernandez-Vazquez, 1994; Smith *et al.* 2001). Where key spawning and nursery areas are spatially decoupled, the optimum spawning grounds are frequently located relatively close to the main nursery areas or utilise prevailing currents to facilitate movement of eggs/larvae from the spawning grounds to the nursery areas (Shelton and Hutchings, 1981; Nelson *et al.* 1994; Hugget *et al.* 1998; Hutchings *et al.* 1998; Castro *et al.* 2000).

The spawning seasons, spawning grounds and juvenile nursery areas of anchovy often coincide with those of sardine (*Sardinops sagax*) (Schwartzlose *et al.* 1999; Smith *et al.* 2001; Ward and Staunton-Smith, 2002). Fluctuations in the relative abundance of sardines and anchovies have been observed in many ecosystems (Schwartzlose *et al.* 1999; Nakata *et al.* 2000). In South Australian waters, Ward *et al.* (2001a) observed increases in the distribution and abundance of anchovy following two large-scale mortalities of sardine and concluded that there may be a competitive interaction between the two species.

The Australian anchovy (*Engraulis australis*) and the sardine are found throughout southern Australian coastal waters where both spawn during summer and autumn (Arnott and McKinnon, 1985; Jenkins, 1986; Fletcher and Tregonning, 1992; Hoedt and Dimmlich, 1995). The timing and duration of the spawning season of anchovy in South Australia has not been fully described. Eggs and larvae of both species have been collected from South Australian shelf waters (Ward *et al.* 2001a), but the relative

importance of shelf waters compared to gulf waters as spawning and nursery areas for anchovy is unknown.

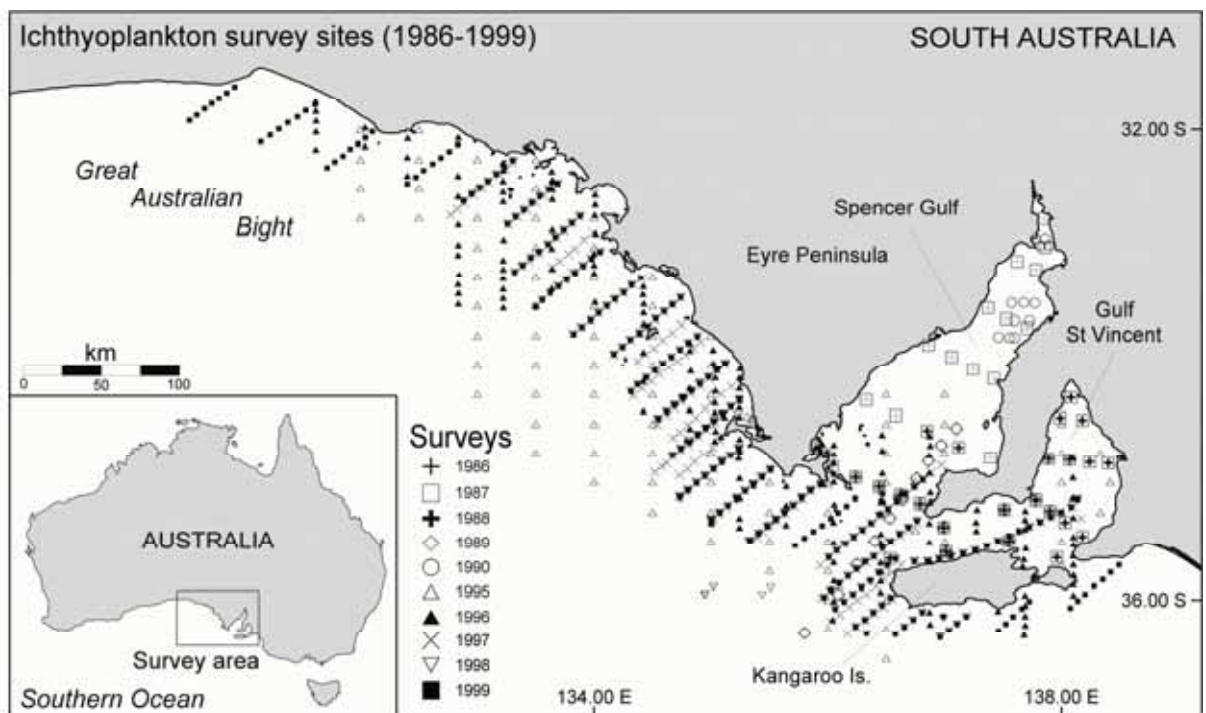


Figure 2.1 Location of all ichthyoplankton sampling sites from 1986 to 1999.

Gulf and shelf waters of South Australia have contrasting hydrographic conditions which may affect the spawning patterns and rates of survival of the eggs and larvae of clupeoids such as anchovies and sardines. Spencer Gulf and Gulf St Vincent (Fig. 2.1) are both inverse estuaries with low to moderate wave energy environments and mean depths of about 20 m (IMCRA 1998). Water temperatures up to 30° C and salinities up to 50 are recorded in the shallow (<10 m) northern reaches of the gulfs during summer and autumn (Bruce and Short, 1990; IMCRA, 1998). As few rivers feed into the gulfs, and there are no other known sources of nutrient enrichment, levels of primary and secondary production are relatively low. During summer and autumn, thermal and saline frontal systems form at the entrances to the gulfs and in Investigator Strait (Fig. 2.2) that effectively delineate gulf and shelf waters (Bruce and Short, 1990).

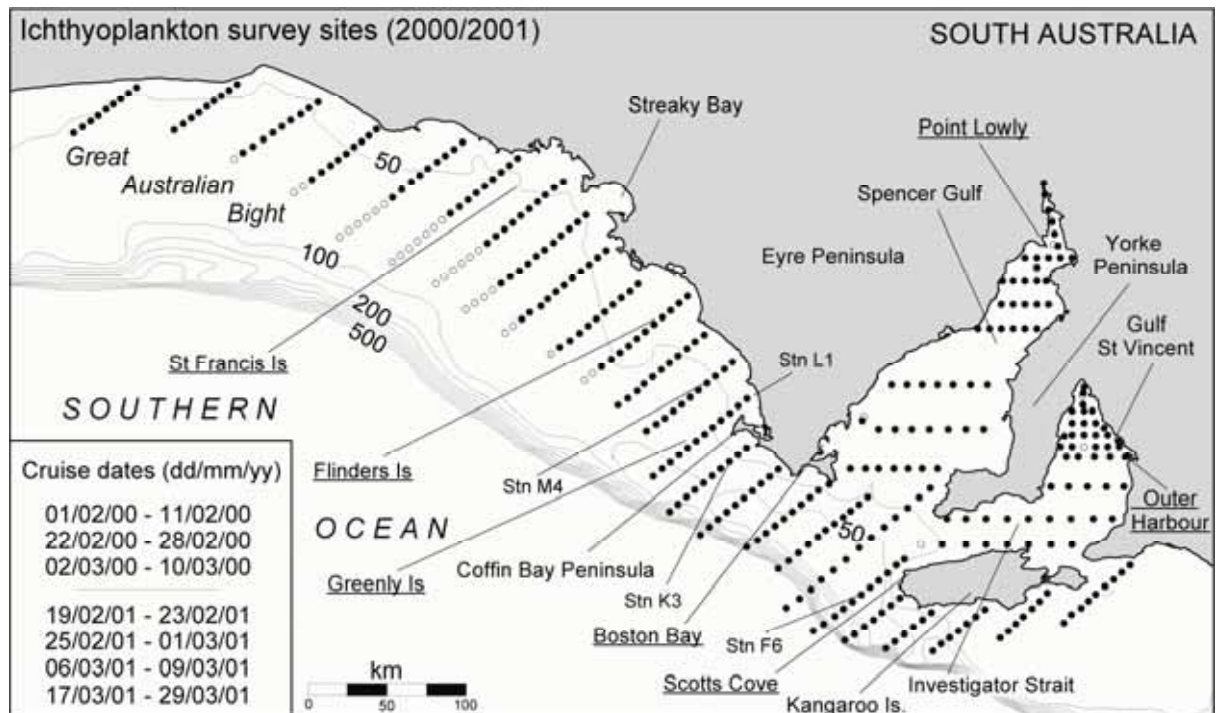


Figure 2.2. Location of ichthyoplankton sampling sites in 2000 and 2001. Open circles (○) identify stations added in 2001. Underlined text indicates adult anchovy sampling locations. Bathymetry contours to 500 m bottom depth are included.

In contrast to the gulfs, shelf waters of the eastern Great Australian Bight are moderate to high wave energy environments. Sea surface temperatures in shelf waters during summer are generally lower than in the gulfs and can be as low as 12° C in coastal waters where primary productivity is enhanced by seasonal upwelling events (Lewis, 1981; Hoedt *et al.* 1996). Sea surface temperatures in shelf waters in the central Great Australian Bight can reach 22° C under the influence of the warm, nutrient-poor Leeuwin Current (IMCRA, 1998).

The objectives of this study are to (1) identify the locations and season of anchovy spawning in South Australia, (2) examine the oceanographic and biotic characteristics of South Australia's gulf and shelf waters during the spawning season for anchovy, including determination of SST and chl *a* levels, and (3) examine the relative importance of gulf and shelf waters for anchovy and sardine spawning and anchovy larval recruitment.

Methods

Spawning season

Ichthyoplankton surveys

Plankton samples were obtained during a series of ichthyoplankton surveys undertaken in Gulf St Vincent and Spencer Gulf waters between 1986 and 1990 (Fig. 2.1) using an obliquely towed bongo net (0.7 m diameter; 500 μm mesh) fitted with two flowmeters. For a complete description of sampling methods see Bruce and Short (1990). Plankton samples were also obtained through surveys conducted from 1995 to 1999 in shelf waters of South Australia (Fig. 2.1) using paired CalVET nets (0.225 m diameter, 300 μm mesh) retrieved vertically. These nets were deployed to within 10 m of the seabed in waters less than 80 m deep and to a depth of 70 m in waters deeper than 80 m and retrieved at approximately 1.0 ms^{-1} . All plankton samples were preserved in 5% formalin seawater solution.

Plankton samples were later rinsed in water and sorted using a dissecting microscope. Anchovy eggs were distinguished from other regional pelagic fish eggs by their elliptical shape (Moser and Ahlstrom, 1985). Larvae were separated from co-occurring clupeid larvae (*S. sagax*, *Spratelloides robustus*, *Etrumeus teres*) by myomere counts, gut length and median fin positions (Neira *et al.* 1998). Mean numbers of eggs and larvae (± 1 SE) per sample per month were determined.

The combination of cruise data from the years 1986-1999 presents analytical difficulties due to differences in surveyed areas and equipment used. However, the cruises were conducted throughout the year, providing baseline information on spawning season of anchovy and the extent of spawning activity in South Australia.

Gonosomatic index

Adult fish were sampled monthly at several locations during the period 2000/2001, mainly near Outer Harbour and Point Lowly (Fig. 2.2). Samples were also obtained opportunistically at a number of shelf areas during surveys conducted from January-March in both 2000 and 2001 (Fig. 2.2). Fish were collected using multipanel gillnets

deployed at night, utilising subsurface lights to attract anchovy schools. A comprehensive description of this technique is provided in Ward *et al.* (2001b). Female fish were measured and weighed and ovaries removed and weighed to establish a gonosomatic index (GSI = ovary weight / ovary free body weight). To compare the effect of season on gonad maturation, an ANCOVA was used with body mass as the covariate.

Gulf and shelf oceanographic surveys

Sampling sites were located throughout gulf and shelf waters of South Australia during February to March, 2000 and 2001 (Fig. 2.2), to cover the extent of spawning activity identified by the 1986-1999 surveys. Shelf transects were aligned perpendicular to the coast and gulf transects were aligned east-west. The survey design for both years was similar except for the lengthening of several shelf transects and the elimination of the westernmost transect in 2001 (Fig. 2.2).

Bottom depth and SST were recorded at each site using hull-mounted instruments. Chl *a* levels were also recorded. In 2000 a 250 ml sample of surface water was collected at each site and filtered using a 0.45 µm Millipore filtration system. The filter and residue were folded, sealed in aluminium foil and immediately frozen. Chl *a* levels were determined later in the laboratory by dissolving the filter residue in acetone and estimating fluorescence using a Sequoia-Turner fluorometer (Model-450) with an excitation wavelength of 440 nm and an emission wavelength of 665 nm. The concentration of chl *a* was calculated according to the method of Parsons *et al.* (1984). In 2001, chl *a* concentrations were recorded throughout the water column at each site using a Chelsea Aquatracker 3 fluorometer incorporated into a Seabird SBE19 CTD. For direct comparison between years chl *a* data were converted to µgL⁻¹.

Temperature (° C) and chl *a* (µgL⁻¹) data obtained from each series of surveys were combined and used to generate spatial plots of sea surface temperature and of chl *a* concentrations for the 2000 and 2001 spawning seasons. These data were plotted using Surfer® surface mapping software, employing a minimum curvature interpolation algorithm.

Egg and larval distributions in gulf and shelf waters***a. Spawning distribution***

For the years 2000 and 2001, plankton samples were collected during February – March at all sites located throughout gulf and shelf waters in South Australia (Fig. 2.2). A total of 691 samples was collected using paired CalVET nets (0.225 m diameter, 300 µm mesh), identical to those used during the 1995-1999 offshore surveys, deployed vertically at shelf stations to within 10m of the seabed prior to retrieval. Wire lengths were digitally recorded during deployment. In shallower gulf waters, inaccessible to the primary research vessel and hence unsuitable for vertical tows, nets were deployed and retrieved obliquely (Fletcher and Tregonning, 1992), with tows averaging 5-10 minutes in duration at a towing speed of approximately 1.5 ms⁻¹. The net was towed to within several metres of the bottom and returned to the surface in a step-wise sequence designed to sample the water column evenly. Because both methods sampled the extent of the water column preferred by engraulid larvae during both night and day (Moser and Pommeranz, 1999; Olivar *et al.* 2001), diurnal vertical movement by larvae was not considered a complicating factor in the analysis of the results. Samples were preserved in 5% formaldehyde seawater solution. These samples were later rinsed in freshwater and all clupeoid eggs and larvae identified and counted.

The volume of water filtered by the nets was calculated by multiplying the distance towed by the surface area of the net mouth. Known wire-lengths provided the distance travelled during vertical hauls. The distance travelled by each net during the oblique tows was estimated using net-mounted flowmeters which were calibrated using the known wire-lengths obtained from the vertical tows. The density (100 m⁻³) of anchovy and sardine eggs and larvae in each sample was calculated using the equation:

$$D = \frac{100 \cdot N}{V} \quad (1)$$

where N is the total numbers of eggs/larvae in each sample and V is the volume of water sampled (m³). Densities, rather than area estimates (eggs m⁻²) were calculated to facilitate comparison with published results for other anchovy studies in Australian

waters.

b. Anchovy larvae size-class distribution

All anchovy larvae collected in the plankton tows during 2000 and 2001 were photographed and measured (TL mm) using SigmaScan™ image analysis software. Larvae were then grouped into four classes by size: <5 mm, 5-10 mm, 10-15 mm and >15 mm. These distributions were then plotted for each year showing numbers of larvae in each size class at each sampled site. Numbers of larvae were used instead of densities to facilitate intra-site comparisons between size-classes.

Results

Spawning season

There was significant variation in the GSI (Fig. 2.3a, $p = 0.025$) which ranged from 0.4 - 5.1% over the period from 2000 to 2001. In general, the GSI was low during May to October, and high from November to March with maxima in February and March.

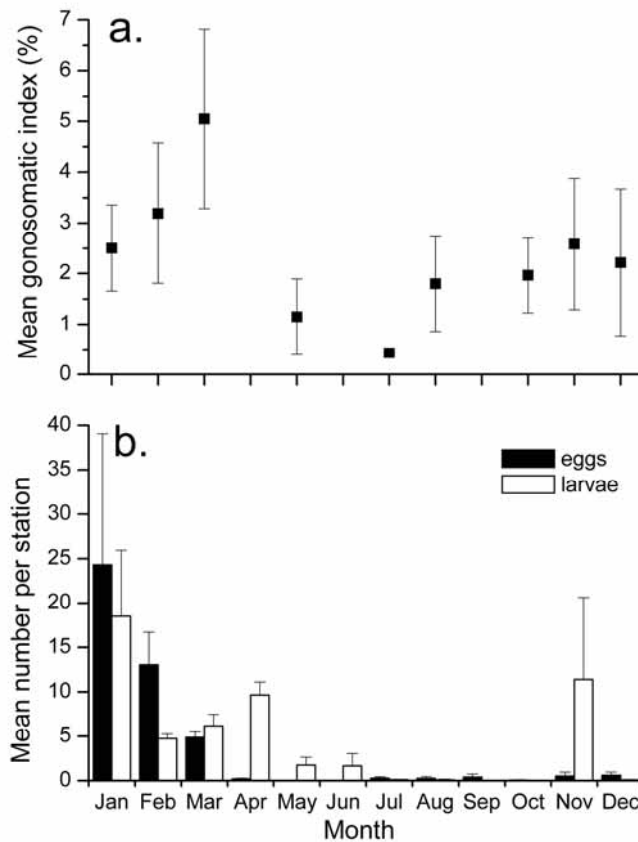


Figure 2.3. a) Monthly gonosomatic index determined on surveys from 2000 to 2001 and b) mean numbers of eggs and larvae per sample (± 1 SE) for anchovy during all surveys from 1986 to 2001

Both the GSI and monthly egg and larval abundances (Fig. 2.3b), obtained from the pooled results of all ichthyoplankton surveys from 1985 to 2001, indicates that the spawning season for anchovy in South Australia commences in late spring (November) and continues throughout summer to early autumn (March) with peak activity occurring between January and March. The presence of eggs and/or larvae in most months indicate that low background levels of spawning activity takes place throughout the year.

Gulf and shelf oceanographic surveys

Sea surface temperatures measured during the cruise periods (February – March) ranged from 16.3 to 26.0°C in 2000 and 16.6 to 26.0°C in 2001 (Fig. 2.4a,b) with the lower temperatures recorded near the Coffin Bay Peninsula and warmer temperatures

in the northern gulf waters. Cooler temperatures were also recorded in both years off the western tip of Kangaroo Island.

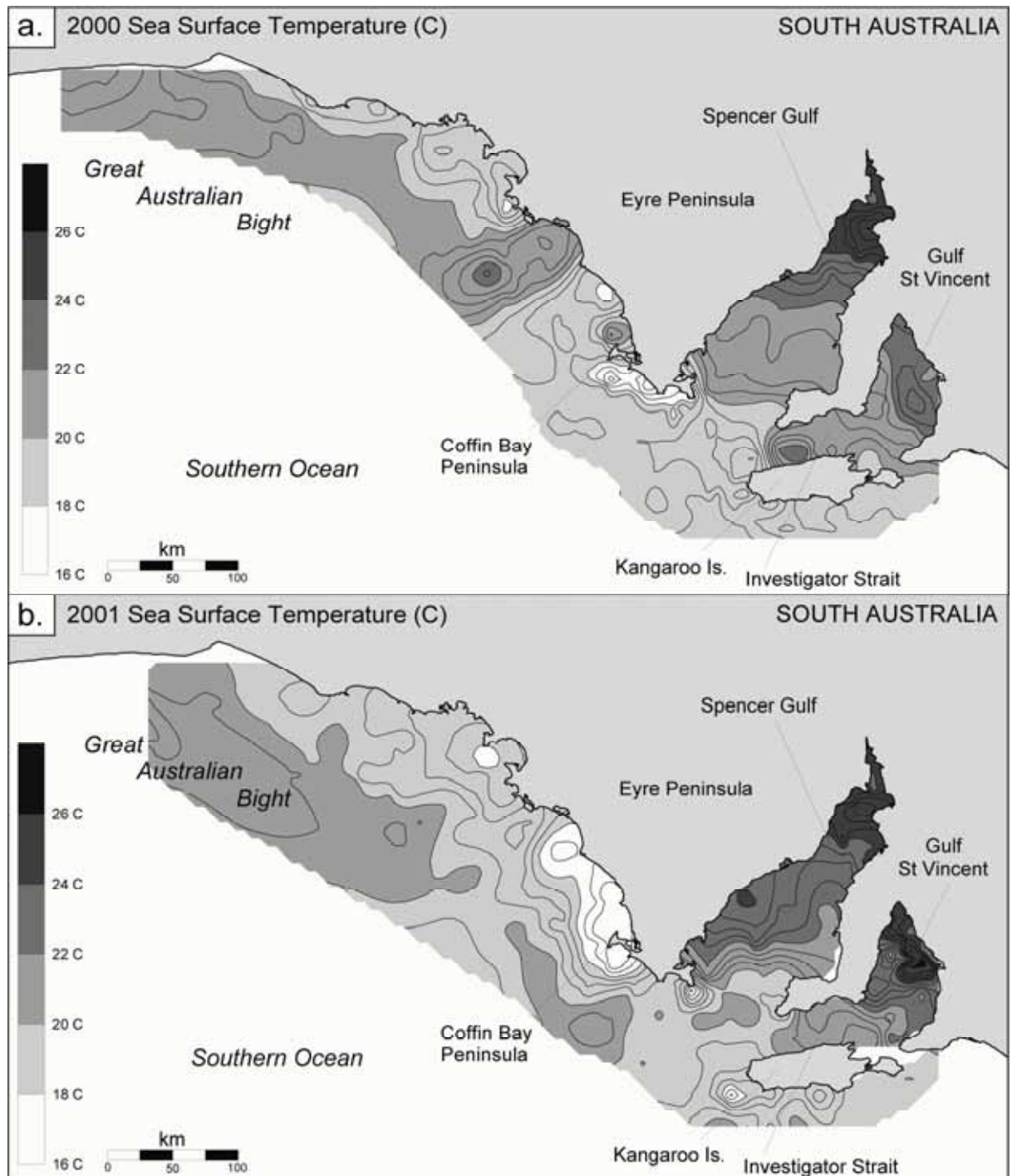


Figure 2.4 Contour plots of combined sea surface temperatures (°C) measured during the 2000 and 2001 cruises. Contour interval is 0.5 °C.

Concentrations of chl *a* during the cruise periods ranged from 0.06 to 1.58 μgL^{-1} in 2000 (Fig. 2.5a) and from 0.40 to 1.12 μgL^{-1} in 2001 (Fig. 2.5b). Concentrations were highest inshore and declined as distance from shore increased. During 2000, high concentrations of chl *a* were recorded around the Coffin Bay Peninsula and in coastal waters of the eastern Great Australian Bight (Fig. 2.5a). Concentrations of chl *a* in 2001 did not attain the same maxima as recorded in 2000 but were distributed more evenly throughout shelf waters (Fig. 2.5b).

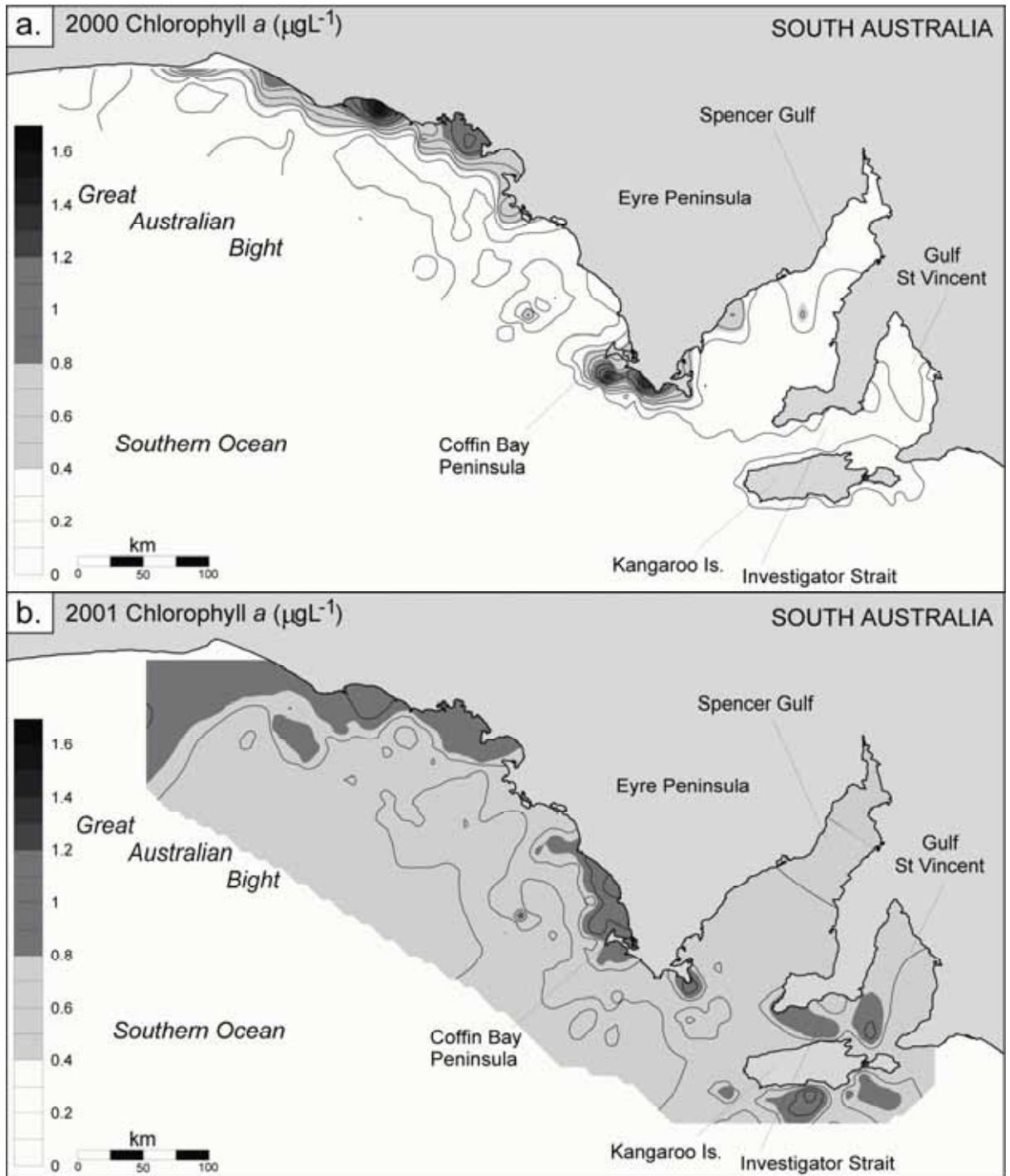


Figure 2.5 Contour plots of combined chlorophyll *a* levels (μgL^{-1}) measured during the 2000 and 2001 cruises. Contour interval is $0.15 \mu\text{gL}^{-1}$.

Egg and larval distribution in gulf and shelf waters.***a. Spawning distribution******Anchovies***

Totals of 6,321 anchovy eggs and 2,639 anchovy larvae were collected from 342 stations sampled in 2000, whereas 1,220 eggs and 1,378 larvae were collected from the 360 stations sampled during the 2001 survey (Table 2.1). Eggs were collected from 37% and 33% of stations in 2000 and 2001 respectively, whereas larvae were present at 54% of stations in 2000 and 51% of stations in 2001 (Fig. 2.6).

Table 2.1. Summary of cruises, *Engraulis australis* numbers and mean densities of anchovy eggs and larvae (± 1 SE) observed in surveyed areas from February and March, 2000 and 2001.

Year	2000	2001
Survey area (km ²)	127,000	156,000
Number of stations	342	360
Volume of water filtered (m ³)	1653	1684
Number of eggs	6321	1220
Number of larvae	2639	1378
Overall mean egg density (100m ⁻³)	368 (83)	119 (21)
Overall mean larval density (100m ⁻³)	168 (25)	147 (17)
Gulf mean egg density (100m ⁻³)	1026 (315)	238 (73)
Gulf mean larval density (100m ⁻³)	383 (90)	266 (64)
Shelf mean egg density (100m ⁻³)	156 (35)	85 (17)
Shelf mean larval density (100m ⁻³)	99 (14)	113 (12)

Mean densities of eggs and larvae were higher in gulf waters than in shelf waters during both years (Table 1) particularly in 2000, when the mean densities at gulf sites (1,026 eggs 100m⁻³ and 383 larvae 100m⁻³) were much higher than mean densities on the shelf (156 eggs 100m⁻³ and 99 larvae 100m⁻³). During 2001, mean densities in the gulfs (238 eggs 100m⁻³ and 266 larvae 100m⁻³) were higher than on the shelf (85 eggs 100m⁻³ and 113 larvae 100m⁻³).

Overall, mean densities of eggs were higher in 2000 (368 eggs 100m⁻³) than in 2001 (119 eggs 100m⁻³) (Table 1). In contrast, mean larval abundances were only slightly higher in 2000 (168 larvae 100m⁻³) than in 2001 (147 larvae 100m⁻³).

The highest absolute egg densities in 2000 were observed in northern gulf waters where maximum densities of 13,942 eggs 100m^{-3} (Spencer Gulf) and 11,571 eggs 100m^{-3} (Gulf St Vincent) were recorded. In contrast, the highest egg density recorded on the shelf was 4,401 eggs 100m^{-3} at station L1 (Fig 6a). During the following year, maxima of only 2,700 eggs 100m^{-3} in Gulf St Vincent and 1,617 eggs 100m^{-3} in Spencer Gulf were recorded (Fig. 2.6b). The highest egg density recorded on the shelf in 2001 was 1,657 eggs 100m^{-3} at station M4 (Fig 6b).

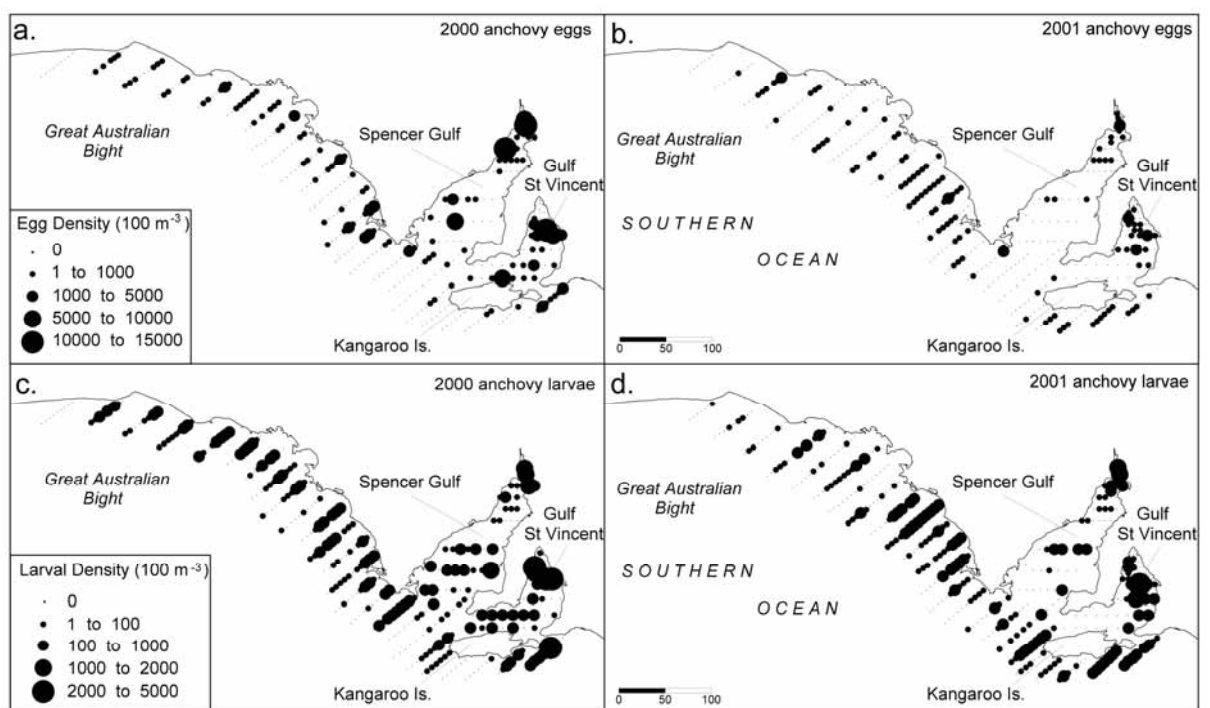


Figure 2.6 Density plots (100m^{-3})⁻¹ of anchovy eggs and larvae during February – March surveys, 2000 and 2001. Significant station locations are indicated in Figure 2.

The highest larval densities in 2000 were also recorded in gulf waters with maxima of 1,765 larvae 100m^{-3} in southern Spencer Gulf (highest density recorded in northern Spencer Gulf was 1,548 larvae 100m^{-3}) and 4,302 larvae 100m^{-3} in northern Gulf St Vincent (Fig. 2.6c). The highest density of larvae recorded on the shelf in 2000 was 844 larvae 100m^{-3} at station K3 (Fig. 2.6c). In 2001, larval densities were lower in gulf waters with maxima of 2,285 larvae 100m^{-3} recorded in Gulf St Vincent and 1,561 larvae 100m^{-3} in Spencer Gulf (Fig. 2.6d). The highest larval density in shelf waters during

2001 was 539 larvae 100m^{-3} at station F6 (Fig. 2.6d).

Sardines

In 2000, totals of 1,362 sardine eggs and 1,418 sardine larvae at mean densities of 135 eggs 100m^{-3} (± 1 SE of 26) and 119 larvae 100m^{-3} (± 22) respectively were recorded. The highest densities recorded in shelf waters were 3,982 eggs 100m^{-3} and 4,401 larvae 100m^{-3} (Fig. 2.7a,c). The following year, totals of 1,402 eggs and 1,975 larvae at mean densities of 210 eggs 100m^{-3} (± 35) and 265 larvae 100m^{-3} (± 35) respectively were recorded. Maximum densities in 2001 were 5,461 eggs 100m^{-3} and 5,354 larvae 100m^{-3} (Fig. 2.7b,d).

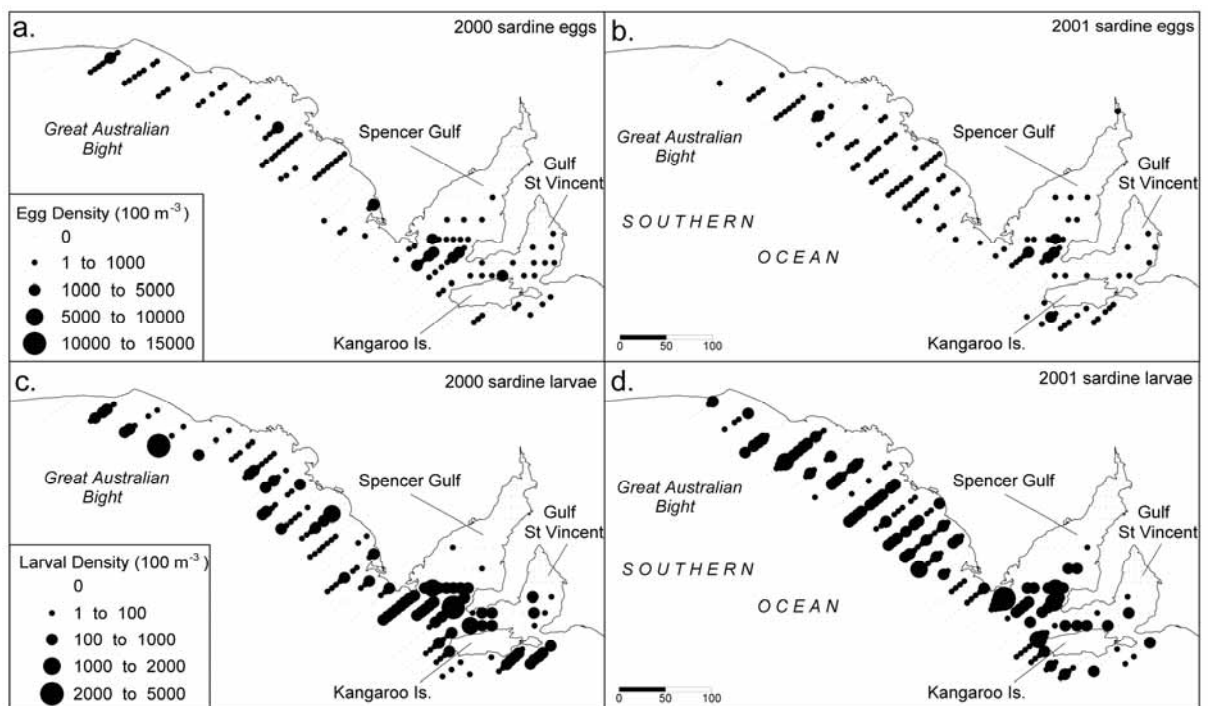


Figure 2.7 Density plots ($(100\text{m}^{-3})^{-1}$) of sardine eggs and larvae during February – March surveys, 2000 and 2001.

There was little evidence of spawning in northern gulf waters by sardines in either year (a single egg was recorded in 2001 in the northern Spencer Gulf) (Fig. 2.7a,b). No sardine larvae were collected from the northern reaches of either gulf (Fig. 2.7c,d). High densities of larvae were observed at the entrance to Spencer Gulf in both years near the

region where thermal frontal zones form during summer months (Fig. 2.4).

b. Anchovy larvae size-class distributions

The distribution of anchovy larvae within size classes of <5mm, 5mm-10mm, 10mm-15mm and >15mm was generally similar between years (Fig. 2.8). Smaller larvae (<5mm) were distributed over the entire survey area (Fig. 2.8a,e) as were larvae of the next size class (5-10mm), although more sparsely (Fig. 2.8b,f). However, larvae >10mm were largely restricted to areas to the north-west of the Coffin Bay Peninsula and off the western point of Kangaroo Island, particularly in 2000. These areas were far removed from areas of maximum spawning activity in the northern gulf areas where the highest egg densities were recorded.

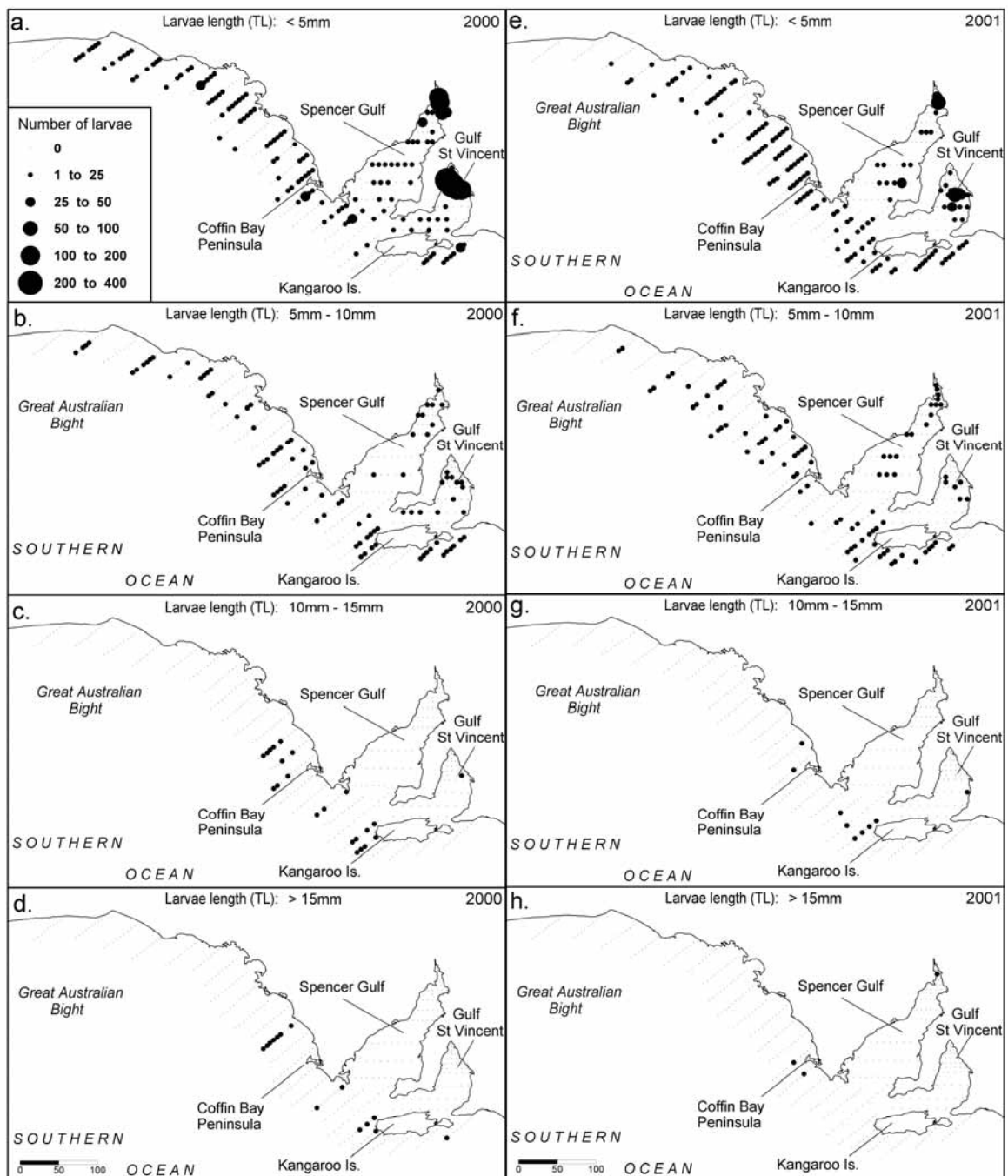


Figure 2.8 Numbers of anchovy larvae of each size class (<5 mm, 5 mm – 10 mm, 10 mm – 15 mm, >15 mm) at each site during February-March surveys, 2000 and 2001.

Numbers of larvae within the smaller size classes were higher in shallower waters while proportionately higher numbers of larger larvae were present in deeper waters (Fig. 2.9a). The numbers of smaller larvae were also higher in warmer waters from 23.5° C to

over 26° C (Fig 2.9b) but were proportionately lower in cooler water below 19° C. There were also relatively high numbers of smaller larvae at approximately 19° C. Low numbers of larvae at all size classes were present in the coolest water (approximately 16° C) recorded within the upwelling zones.

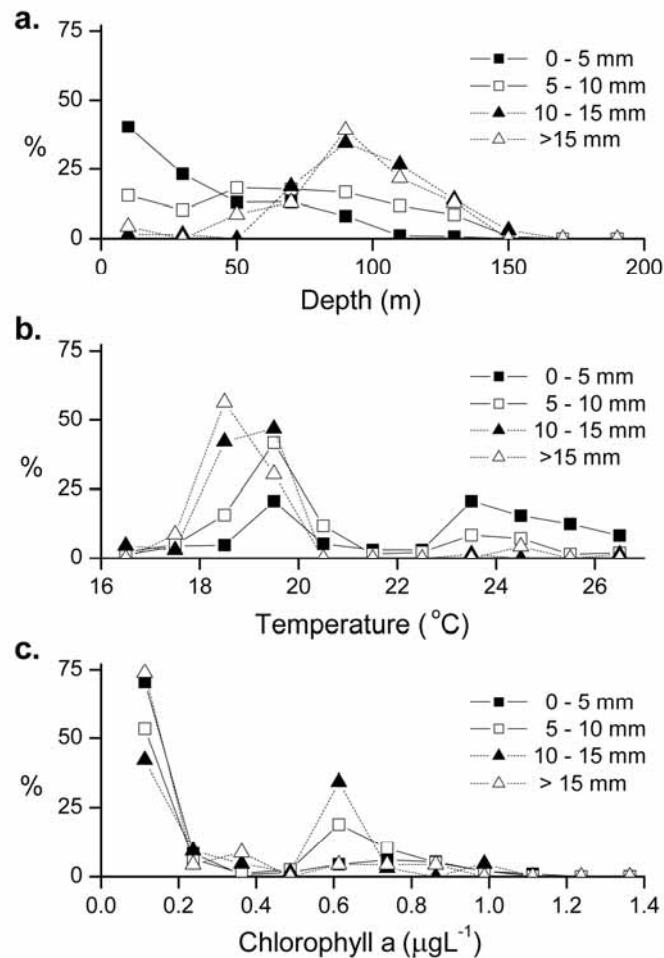


Figure 2.9 Proportions (% of total) of anchovy larvae of different size classes at differing a) depths, b) sea surface temperatures and c) surface chl *a* concentrations, aggregated from February – March surveys, 2000 and 2001.

Larvae of 3 mm TL dominated catches in both years (Fig. 2.10). No larvae caught were less than 2 mm TL, this approximating the length at hatch and representing the minimum size of larvae available for sampling. Numbers increased from 2 mm to 3 mm, suggesting that some extrusion of smaller larvae through the net mesh is occurring at lengths below 3 mm. Numbers of larger larvae declined rapidly to approximately 13 mm

(Fig. 2.10), from which catches remained consistently low to 20 mm. At 21 mm and greater, 100% of larvae were able to evade capture by the nets.

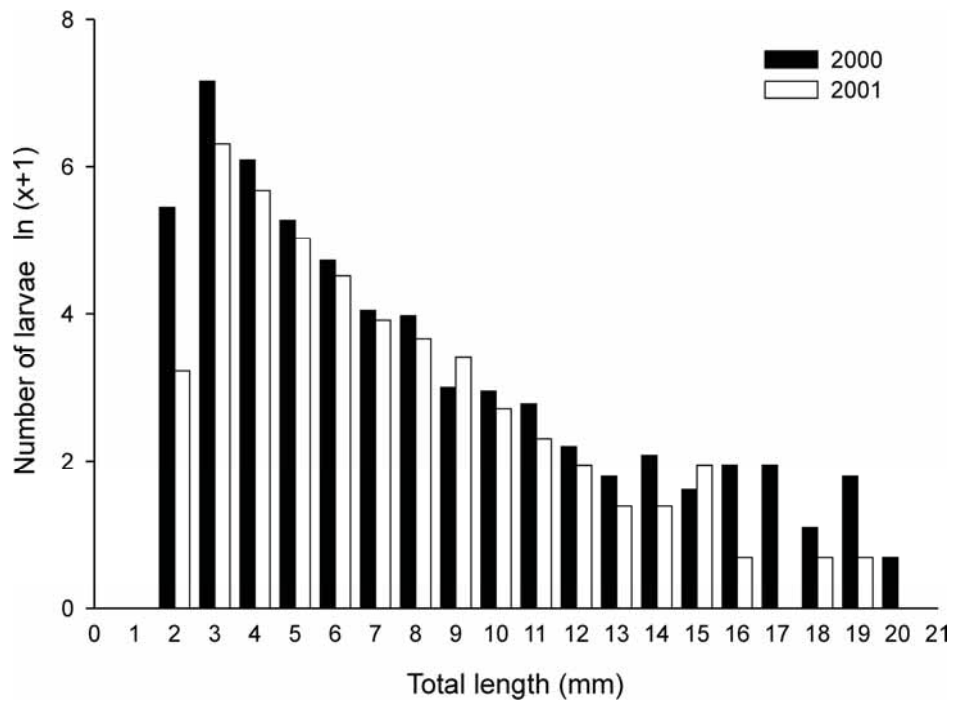


Figure 2.10 Numbers of anchovy larvae at different sizes captured during the February – March ichthyoplankton surveys, 2000 and 2001.

Discussion

The spawning season of anchovy in South Australia occurs during summer and autumn when seasonal upwelling events occur along the coast of the western Eyre Peninsula and the western tip of Kangaroo Island. Differences in spawning peaks between egg abundance estimates and the GSI are probably due to interannual variations in spawning activity. The egg densities were a composite of all years sampled from 1986 to 2001 while the GSI's were derived over a shorter period from 2000 to 2001. Both, however, identified a period of peak spawning during January to March and this period has also been identified as the peak spawning season of sardine in South Australia (Ward *et al.* 1998). The spawning season of engraulids in other ecosystems frequently coincide with upwelling events, whether they occur in winter, *E. ringens* (Chesney and Alonso-Noval, 1989; Castro *et al.* 2000), spring, *E. mordax* (Hernandez-Vazquez, 1994)

or summer, *E. encrasicolus* (Shelton and Hutchings, 1981; Roy *et al.* 1989; Beckley and Hewitson, 1994; Lafuente *et al.* 2002). Correlation of spawning with upwelling events suggests that local primary productivity (Brown, 1984; Olivieri and Hutchings, 1987) indirectly supports large assemblages of clupeoid fishes (Daneri *et al.* 2000; Morales *et al.* 2001).

Anchovy eggs were collected throughout gulf and shelf waters, but the highest densities of eggs were recorded in the northern gulfs, where SSTs during summer and autumn approached 26° C. Maximum spawning activity at temperatures above 20° C have also been reported for *E. encrasicolus* (King, 1977; Niermann *et al.* 1994; Van der Lingen, 2001), *E. mordax* (McGowan, 1986) and for the Australian anchovy in southern Queensland (Ward *et al.* 2003). The maximum egg density recorded in northern gulf waters (13,942 eggs 100m⁻³) was among the higher egg densities recorded in other populations of Australian anchovy where nets of 300µm mesh or less were used: 38,200 eggs 100m⁻³ in Gippsland Lakes, Victoria (Arnott and McKinnon, 1985); 15,000 eggs 100m⁻³ in Port Phillip Bay, Victoria (Jenkins, 1986); 625 eggs 100m⁻³ in Western Port, Victoria (Hoedt and Dimmlich, 1995); 1,626 eggs 100m⁻³ in Wilson's Inlet, Western Australia (Neira and Potter, 1992). Hence, environmental conditions in the northern gulf areas appear to support higher than average levels of spawning activity for anchovy in Australian waters.

Small larvae (<5 mm TL) representing the first stage of development post-hatch were also collected throughout gulf and shelf waters, although overall densities were considerably lower than egg densities. This is probably due to high mortality rates of young larvae (Smith, 1985). Reductions in larval abundance relative to size were consistent throughout the survey area for larvae up to 10mm in length.

Larvae >10 mm were captured in areas located near upwelling zones to the west of southern Eyre Peninsula and to the west of Kangaroo Island, but not in the gulfs or in shelf waters west of Streaky Bay. As capture rates of large larvae were expected to be low due to their higher capacity for net avoidance (Hewitt and Brewer, 1983; Smith, 1985; Moser and Pommeranz, 1999), this result does not indicate that large larvae were

completely absent from the gulfs or western shelf waters, but implies that they were present in considerably higher densities in the upwelling zones. The absence of large larvae in the samples obtained from northern gulf regions is particularly significant since the oblique tows employed in those shallow waters were faster, sampled the water column twice during net deployment and retrieval and were of longer duration, filtering more water than the deeper vertical tows. Furthermore, the high turbidity of northern gulf waters should have resulted in more captures due to reduced evasion levels but this was not evident in our results.

High inter-annual variations in abundances of eggs have previously been reported for Australian anchovy (Hoedt and Dimmlich, 1995, Ward *et al.* 2001a) with poor correlations between densities of eggs and subsequent densities of larvae. In the present study, egg densities differed significantly between 2000 and 2001, yet larval densities were similar between years. Comparable patterns have been reported in other studies, eg. Arnott and McKinnon (1985) reported egg densities of up to 38,200 eggs 100m^{-3} in the Gippsland Lakes, but suggested that larval densities rarely exceeded 100 larvae 100m^{-3} , indicating a weak association between egg and larval densities in areas that may be conducive to spawning but less favourable for larval survival. This suggests that areas of higher abundance of larger larvae rather than high egg densities may characterise the most favourable nursery areas.

The survival rates of larvae in the >10 mm size range can determine the levels of recruitment into the juvenile stage of anchovies such as *E. mordax* (Peterman *et al.* 1988). The recruitment success of several species including *E. encrasicolus* can be limited by the strength of upwelling processes that drive nutrient enrichment (Cole and McGlade, 1998). The present study suggests that upwelling processes may also affect the recruitment success of anchovy in South Australian waters.

Limited prey availability may reduce larval survival rates in years of higher egg production of *E. mordax* (McGowan, 1986). The distribution of the larvae of some species of anchovies (eg. *E. encrasicolus*) has been associated with the availability of suitable food organisms (Palomera, 1991). Positive correlations have also been found

between concentrations of chl *a* and densities of *E. ringens* larvae (Sameoto, 1982; Rojas *et al.* 2002). Nutrient levels off southern Australia are generally low and rates of larval mortality may be high due to reduced probability of larvae encountering or remaining in patches of suitable prey items (Gaughan *et al.* 2001). Shelf waters of South Australia are one of the few locations in southern Australia where productivity is enhanced by large-scale, predictable, nutrient enrichment processes. The high densities of large larvae recorded to the west of the southern Eyre Peninsula and to the west of Kangaroo Island may reflect high concentrations of prey items in these areas.

The critical scales of oceanic features which concentrate food at levels necessary for larval *E. mordax* survival are approximately 27 km across if food is required for a week and 147 km across if the food is required for a month (Smith and Hewitt, 1985). Although prey concentrations and diffusion away from upwelling zones may differ in South Australia from those reported in Californian waters, oceanographic features (i.e. upwelling zones) at comparable scales, which may be required for longer term feeding and growth of anchovy larvae and which persist for several months, only occur in shelf waters to the west of the southern Eyre Peninsula and Kangaroo Island. Spawning grounds to the west of Streaky Bay are outside the main upwelling zones, and gulf waters are separated from the upwelling zones by frontal systems (Bruce and Short, 1992) and distance. The negative consequences of a laterally incoherent and dissipated habitat mainly affect late larval (and juvenile) stages (Smith and Hewitt, 1985), which corresponds with the stage when larval abundance declined rapidly in the present study. Upwelling strength and the size of upwelling zones vary between seasons and can affect rates of larval survivorship, recruitment success and age-class strength (Shelton and Hutchings, 1981; Roy *et al.* 1989; Cole and McGlade, 1998).

Although gulf waters support the highest levels of anchovy egg production, upwelling zones appear to provide the more favourable environments for recruitment of anchovy larvae to post larval stages. Successful recruitment of anchovy has been linked to passive transport mechanisms which convey eggs and larvae from warm-water spawning areas to cold-water nursery grounds (Hugget *et al.* 2003). In the northern Spencer Gulf an almost closed circulation system exists (Bullock 1975), concentrating

eggs and larvae in this area and preventing advection of spawning products to southern gulf regions. Where there is no transport mechanism separating spawning products from spawners, cannibalism of eggs and yolk-sac larvae may become a significant factor (Valdes-Szeinfeld and Cochrane, 1992), limiting recruitment to later developmental stages in this area through elevated mortalities.

Predation by sardines can also significantly impact the survivorship of the eggs and larvae of anchovies (Santander *et al.* 1988; Smith *et al.* 1989). The apparent increase in the distribution and abundance of anchovy resulting from two mass mortalities of sardine (Ward *et al.* 2001a), in conjunction with results from the present study, suggests that sardine abundance may affect the survival rates of anchovy larvae in shelf waters of South Australia.

The anchovy population in South Australia appears to be relatively small in comparison to anchovy populations in very productive upwelling zones such as the California, Humboldt and Benguela systems. However, the reciprocal relationships observed between the abundances of anchovies and sardines in those highly productive pelagic ecosystems is also evident in less productive South Australian waters. The anchovy in South Australia is an opportunistic species that appears to be able to rapidly fill a vacant niche provided by a decrease in the local sardine population. We hypothesise that anchovy larvae may effectively utilise the upwelling zones outside the gulfs only when levels of sardine abundance in shelf waters are low. The warm northern and mid-gulf waters, which lie outside the range of temperatures tolerated by sardines (Van der Lingen, 2001, Ward *et al.* 2003), appear to act as marginal spawning and nursery areas for anchovy, and may be critical for sustaining the South Australian anchovy population during periods when sardine abundance is high.

Chapter 3

AGE-STRUCTURED REPRODUCTIVE STRATEGY OF AUSTRALIAN ANCHOVY (*ENGRAULIS AUSTRALIS*) DETERMINED BY OTOLITH MICROSTRUCTURE ANALYSIS.

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Statement of Authorship

Age-structured reproductive strategy of Australian anchovy (*Engraulis australis*) determined by otolith microstructure analysis.

Marine and Freshwater Research, 2006: 57, pp. 373-381.

DIMMLICH, W.F. (Candidate)

Conducted fieldwork, performed analysis on all samples, interpreted data, primary and corresponding author of paper.

I hereby certify that the statement of contribution is accurate

SignedDate...30/4/2010..

WARD, T.M.

Supervised development of research plan, data analysis and interpretation and manuscript development.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis

SignedDate...10.5.10.

Abstract

Upwelling systems can provide ideal conditions for survival and growth of larval fishes. However, these unstable environments are highly dispersive and mortalities can be high. Anchovies (*Engraulis* spp.) utilise a range of behavioural strategies to increase egg and larval survival. Ontogenetic shifts in distribution have been proposed for Australian anchovy (*Engraulis australis*), but no supporting otolith-based age studies have been published to date. The present study used otolith increment counts to age larval, juvenile and adult Australian anchovy, which spawn throughout South Australian gulf and shelf waters. Only fish up to 1 year of age occurred in the northern Spencer Gulf, where eggs and larvae in high densities are retained in a nursery area favourable to anchovies. The southern gulf area was inhabited by 1, 2 and 3 year olds. Older anchovy were found in offshore shelf waters, where upwelling occurs and larval survivorship may be high. We hypothesise that Australian anchovy move offshore with age to utilise the wide range of environments that provide suitable spawning and nursery areas for this species.

Extra keywords: age, growth, nursery areas, reproductive strategy, spawning, upwelling

Introduction

The abundance and distribution of small pelagic fishes occurring in coastal upwelling systems fluctuate in response to environmental or biotic factors acting on early stages, particularly the larvae (Wroblewski 1984; Cole and McGlade 1998; Rojas *et al.* 2002). Advective loss of larvae and eggs in such systems is considered a key factor in determining recruitment levels. Clupeoid fishes are particularly abundant in productive coastal upwelling regions and have developed complex reproductive strategies in response to these dynamic pelagic environments (Bertrand *et al.* 2004; Robinson 2004). Anchovies (*Engraulis* spp.) in particular have adopted flexible behaviours to maximise recruitment in such environments (Shelton and Hutchings 1981; Palomera 1992; Hugget *et al.* 2003; Wilhelm *et al.* 2005). Several studies have suggested that components of adult anchovy populations do not spawn indiscriminately but tend to spawn under conditions and at levels that yield consistent survival probabilities for

their offspring (Owen *et al.* 1989).

The Australian anchovy (*Engraulis australis*) is widely distributed throughout temperate Australian coastal waters, south of the Tropic of Capricorn (Blackburn 1950; Hobday 1992; Hoedt *et al.* 1995) (Fig. 3.1). South Australia lies at the centre of this distribution and anchovy eggs, larvae and adults have been recorded throughout gulf and shelf waters with spawning occurring during summer-autumn (Ward *et al.* 2001; Dimmlich *et al.* 2004).

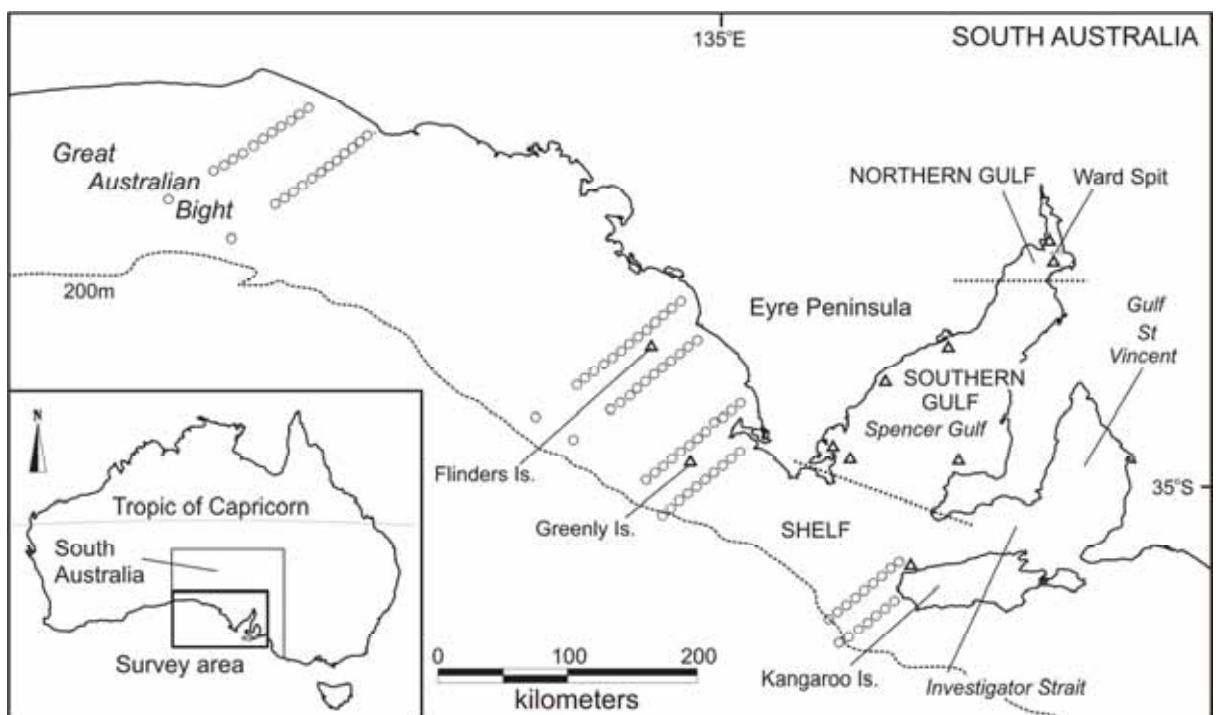


Figure 3.1 Regions used in study. Circles indicate ichthyoplankton sampling stations. Triangles indicate juvenile/adult sampling sites.

The coastal oceanography of South Australian waters is complex, comprising two large gulfs which are inverse estuaries during summer and a broad shelf over which pelagic production is enhanced throughout summer-autumn by upwelling of cool nutrient-rich water (Kampf *et al.* 2004). Southern gulf areas are characterised by temperature and salinity frontal zones which may act to separate gulf and shelf waters during summer-autumn (Bruce and Short 1990). No information is available on the age structure of the anchovy populations that spawn in these two environmentally distinct locations (Ward

et al. 2001; Dimmlich *et al.* 2004).

There have been numerous studies of the age and growth of anchovies in other ecosystems, where they are economically important (e.g. Melo 1984; Bellido *et al.* 2000; Cuttita *et al.* 2003; Basilone *et al.* 2004), but relatively few studies in Australia where exploitation rates are low. Growth increments in scales were used in early aging studies (e.g. Blackburn 1950) but this method of age determination has declined in favour of otolith-based methods in recent years after several studies showed that scale-based approaches may underestimate the ages of clupeids and other fish species (Pertierra and Morales-Nin 1989; Francis *et al.* 1992; McFarlane and Beamish 1995).

Otolith-based age-determination methods assume that growth increments are formed regularly (Begg *et al.* 2005) and the experimental validation of increment periodicity for individual species has often verified the accuracy of this method. However, validation of increment formation periodicity in anchovies has proven difficult. Captive rearing studies have been attempted to validate the timing of increment formation for young anchovy (Methot and Kramer 1979), but the sensitivity of the species to capture and transport have limited the feasibility of using direct validation methods for determining increment periodicity in older fish. On the few occasions when adult anchovy have been successfully maintained for extended periods, results suggest that the daily rhythm of increment formation can be lost, resulting in the underestimation of age (Cermenio *et al.* 2003). Consequently, captive rearing has been generally discounted as a reliable approach for annuli validation for anchovies (Campana 2001). Marginal increment analysis (MIA) has also proven to be problematic because the edges of anchovy otoliths are often difficult to interpret, thus introducing a significant element of subjectivity into the analyses (Melo 1984, Campana 2001).

For fast-growing, short-lived species, such as anchovy, length-based methods have been identified as a suitable option for corroborating the timing of increment formation (Campana 2001). Length-based modules provided by the software package FiSAT (Gayanilo and Pauly 1997) have routinely been used to estimate growth parameters for adult clupeoids (Beverton 1963; Pauly and David 1981; Prosch 1986) and to

corroborate increment-based estimates of age for anchovies (Morales-Nin and Pertierra 1990; Basilone *et al.* 2004).

In Australia, Blackburn (1950) used growth increments in the scales as a basis for concluding that *E. australis* remains in bays and inlets until 2.5 years of age before adopting a 'duo phase' lifecycle, inhabiting offshore waters throughout the year and moving into embayments to spawn during summer. In the absence of new information, these age estimates are still being used for this species (eg. Taylor and Roe 2004) and the hypothesis that adult anchovies move into embayments to spawn has not been discounted.

Relatively small, spawning *E. australis* have been collected from Western Port Bay, Victoria (Hoedt *et al.* 1995) and larger anchovies have been captured in deeper waters off Western Port Bay (Hobday 1992). These results have been used to suggest that the age and size of *E. australis* increases with distance from shore, and used to support Blackburn's hypothesis that large (old) anchovies make annual migrations into shallower bays and inlets to spawn (Hobday 1992; Hoedt *et al.* 1995). However, these studies did not estimate the age of anchovies directly, but based their conclusions on the unvalidated, scale-based estimates of age-at-length provided by Blackburn (1950).

The present study is the first since Blackburn (1950) to directly examine the age and growth of *E. australis*. The aims of this study are: 1) to assess and compare estimates of age and growth rates of larval, juvenile and adult anchovies obtained from increment analysis and length-based methods; 2) to compare the age and size structures of anchovy in northern Spencer Gulf, southern Spencer Gulf and shelf waters of South Australia, and 3) to compare our estimates of size-at-age with those provided for comparable environments by Blackburn (1950), Hobday (1992) and Hoedt and Dimmlich (1995).

Materials and methods

Sampling

Engraulis australis larvae were collected using paired conical plankton nets (diameter 0.6 m, mesh size 500 µm) at offshore sites (Fig. 3.1) during February and March 2002. Nets were towed obliquely within 20m of the surface at vessel speeds of approximately 4 knots. Anchovy larvae have been shown to have a shallow vertical distribution even in deeper waters (Sameoto 1982; Palomera 1991; Moser and Pommeranz 1999). Samples were immediately preserved in 70% ethanol. Plankton samples were sorted using a dissecting microscope and anchovy larvae were separated from co-occurring clupeoid larvae (*Sardinops sagax*, *Spratelloides robustus* and *Etrumeus teres*) by comparisons of myomere counts, gut lengths and median fin positions (Neira *et al.* 1998). Larvae were photographed under stereomicroscope and total lengths (TL) were measured to the nearest 0.1 mm using SigmaScan™ image analysis software.

Post-larval stages were collected from the surface at night under lights using hand-nets (mesh size 1 mm) at locations in Spencer Gulf, Kangaroo Island and a number of offshore shelf locations (Fig. 3.1) and immediately preserved in 70% ethanol.

Juvenile and adult fish were collected monthly from January to December during 2001 using a multi panel gillnet deployed under lights at night at locations in gulf and offshore areas (Fig. 3.1). The sites were located in similar water depths of less than 30 m and similar distances from either the mainland or offshore islands. The gillnet was comprised of three panels of each of three sizes of multi-filament nylon mesh (Double Diamond: ply-210/4; meshes: 25 mm, 28 mm and 32 mm). A comprehensive description of this technique is provided in Ward *et al.* (2001). The fish were frozen after collection. Sites from which anchovies were collected were assigned one of three broad regional classifications: northern gulf, southern gulf and shelf (Fig. 3.1). These regions were selected to approximate the environments for which previously published information on anchovies in Australia was available.

Fish were measured to the nearest millimetre to obtain standard lengths (SL), fork lengths (FL) and total lengths (TL), weighed whole (g) and assigned to one of 5 maturity

classes based on external morphology of the gonads (Hoedt *et al.* 1995).

Historical data

In order to make ageing and distribution comparisons with previous studies of *E. australis* it was necessary to re-examine historical data published for regions which were similar to those defined in the present study. Blackburn's (1950) data obtained in Port Phillip Bay from October 1943 to February 1944 was digitised and converted from standard lengths (SL) to TL using the calculated relationship $TL = 1.14SL + 2.76$ (Unpublished data, $R^2 = 0.95$). Frequencies were converted to percentages of the total number of fish caught over that period. Anchovy length frequency distributions for Bass Strait obtained from October 1986 to February 1987 were digitised from Hobday (1992). Fork lengths (FL) were converted to TL using the relationship $TL = 1.09FL + 0.66$ (Unpublished data, $R^2 = 0.98$). The raw data in mm (TL) obtained in Western Port by Hoedt *et al.* (1995) was available for the months October 1993 to January 1994. These transformed data were then plotted on common axes for visual comparisons between historical and current regions. Size-selectivity of sampling gear at smaller fish sizes precluded the use of statistical comparison tests.

Otolith analysis – larvae and juveniles

The frozen anchovies were thawed before sagittae were removed, air-dried and fixed to a glass slide using translucent thermoplastic cement (Crystal Bond®). Whole sagittae from larvae and post-larvae were examined using transmitted light under a compound microscope, using oil immersion when necessary.

Sagittae from older juvenile fish required further processing before aging could be attempted. These were embedded concave surface facing upwards in a small amount of cement and ground using progressively finer grades of lapping film until the primordium and surrounding growth increments became visible. The cement was reheated and the sagittae turned over and re-embedded. The second side was also ground, polished, and a final protective layer of translucent cement was applied in lieu of a cover-slip.

Concentric rings observed in sagittal sections from post-larval and juvenile fish were assumed to be daily growth increments, as validated for *Engraulis spp.* by Castello and Castello (2003) and Cermeno *et al.* (2003). Counting followed the path of clearest increment formation from the primordium outwards to the posterior otolith margin. When the increment pattern failed along a particular counting axis, the last distinct increment was followed laterally and counting resumed along the next clear increment sequence. Three replicate counts were made and the mean of these counts used to age each individual fish.

The Laird-Gompertz growth model was used to describe the relationship between age (days) and length for larvae and is represented by:

$$L(t) = a \exp\left(\frac{b}{c} [1 - \exp(-c(t - t_0))]\right) \quad (1)$$

where $L(t)$ is the length at age t , a is length at age t_0 , b is the specific growth rate at age t_0 , and c is the rate of exponential decay of the growth rate. Fitting of the curve was achieved using the Levenberg-Marquardt non-linear curve fitting routine provided by TableCurve2D[®]. Instantaneous growth rates were calculated from the first derivative of the Laird-Gompertz growth equation at daily age intervals.

Growth of juvenile fish post-metamorphosis was best described by a linear model, regressing age (days) against length (mm).

Otolith analysis - adults

For adult anchovies (approx. >100 mm TL), whole otoliths were immersed in water and examined under magnification using side illumination against a dark background. Complete pairs of opaque and translucent zones were considered to represent a single year of growth as validated for *Engraulis encrasicolus* by Waldron (1994). Annual increments were identified on the basis of a pattern of regularly decreasing spacing with age, and increments that were clearly distinguished around the greater part of the posterior of the otolith.

For adult anchovies the von Bertalanffy growth function (VBGF) was used to estimate growth parameters using the age-at-length estimates obtained from otolith interpretation. The von Bertalanffy growth equation is

$$L(t) = L_{\infty} [1 - \exp(-k(t - t_0))] \quad (3)$$

where $L(t)$ is the length in mm at time t (years), L_{∞} the asymptotic length, k is a coefficient of growth and t_0 is the theoretical age at which an anchovy would have been zero length. The growth parameters L_{∞} and k were estimated by minimising the sum of squares using the Solver function of Excel™ for the observed ages of anchovies in years. The 0+ fish were replaced for the purposes of this calculation by the larval and post-larval fish which had been aged more accurately using daily increments.

Length-based analysis

Length-frequency analysis was employed as an independent means of corroborating the age-length relationships obtained from the otolith-based age determinations (Morales-Nin 1989; Morales-Nin and Pertierra 1990; Basilone *et al.* 2004). The ELEFAN I module of the FiSAT II stock assessment package (Gayanilo and Pauly 1997) was used to estimate the growth parameters L_{∞} and k for anchovy during 2001 using monthly pooled length frequencies.

Length at maturity

Values for length at first maturity were estimated by fitting the logistic function to the percentage of females in each 2 mm class interval with ovaries at maturity stages III - V (Hoedt and Dimmlich 1995). Fish with gonads at these stages were undergoing sexual maturation or were in spawning condition or had recently spawned. The curve was fitted using the equation

$$P_L = \frac{1}{[1 + e^{(a+bL)}]} \quad (4)$$

using the Solver function of Excel™, where P_L is the proportion of fish with mature gonads at length interval L , a and b are constants and L_{50} or length when 50% of fish are

mature = $-a/b$.

Results

Length-frequency

All data from the three regions sampled (see Fig. 3.1) was pooled to examine the length structure of the population (Fig. 3.2). There were two distinct size modes at 85 and 115 mm, possibly representing 0+ and 1+ cohorts respectively. Distinct size modes could not be identified in fish >130 mm TL due to length overlap in the older age classes. The largest fish measured was 152 mm TL.

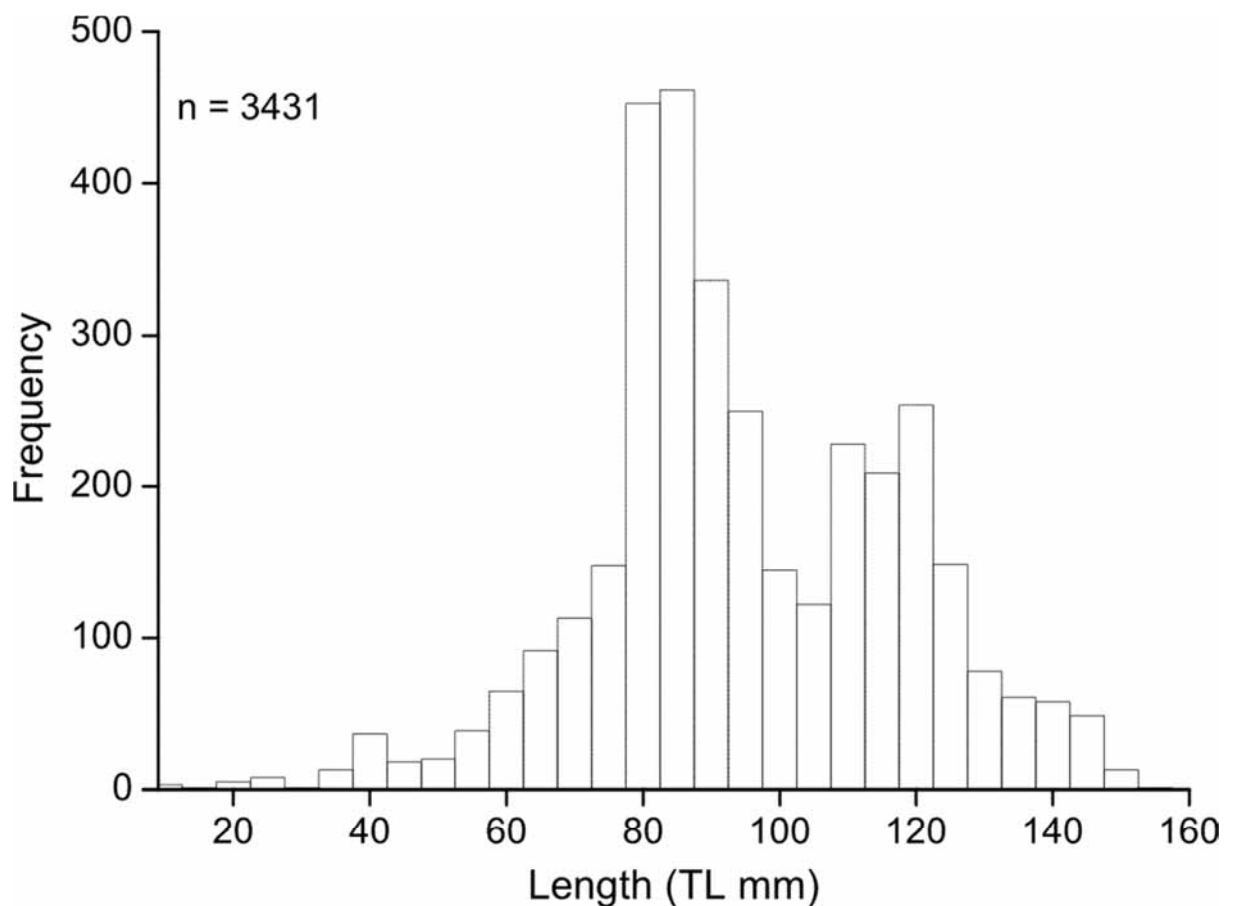


Figure 3.2 Length/frequency of combined *Engraulis australis* measurements from all surveyed regions.

Length-frequency histograms for each month were produced from the pooled adult and post-larval data (Fig. 3.3). The modal size range was between 10 and 150 mm. The first mode following the summer spawning period occurred in February at 20 mm.

Increasing modal lengths presumably representing the developing 0+ group first observed in February were observed from August (60 mm) to January (100 mm), possibly reflecting a cohort growth rate of approximately 0.25 mm day⁻¹ or 8.0 mm month⁻¹ over that period. Additional modes at longer lengths observed in May to August, October to November and March probably represent older cohorts. No adult fish were captured in April, though modes at 110 and 120 mm were present in March and May respectively. A small number of 10 mm larvae were observed in June which falls outside the main spawning season in summer-autumn.

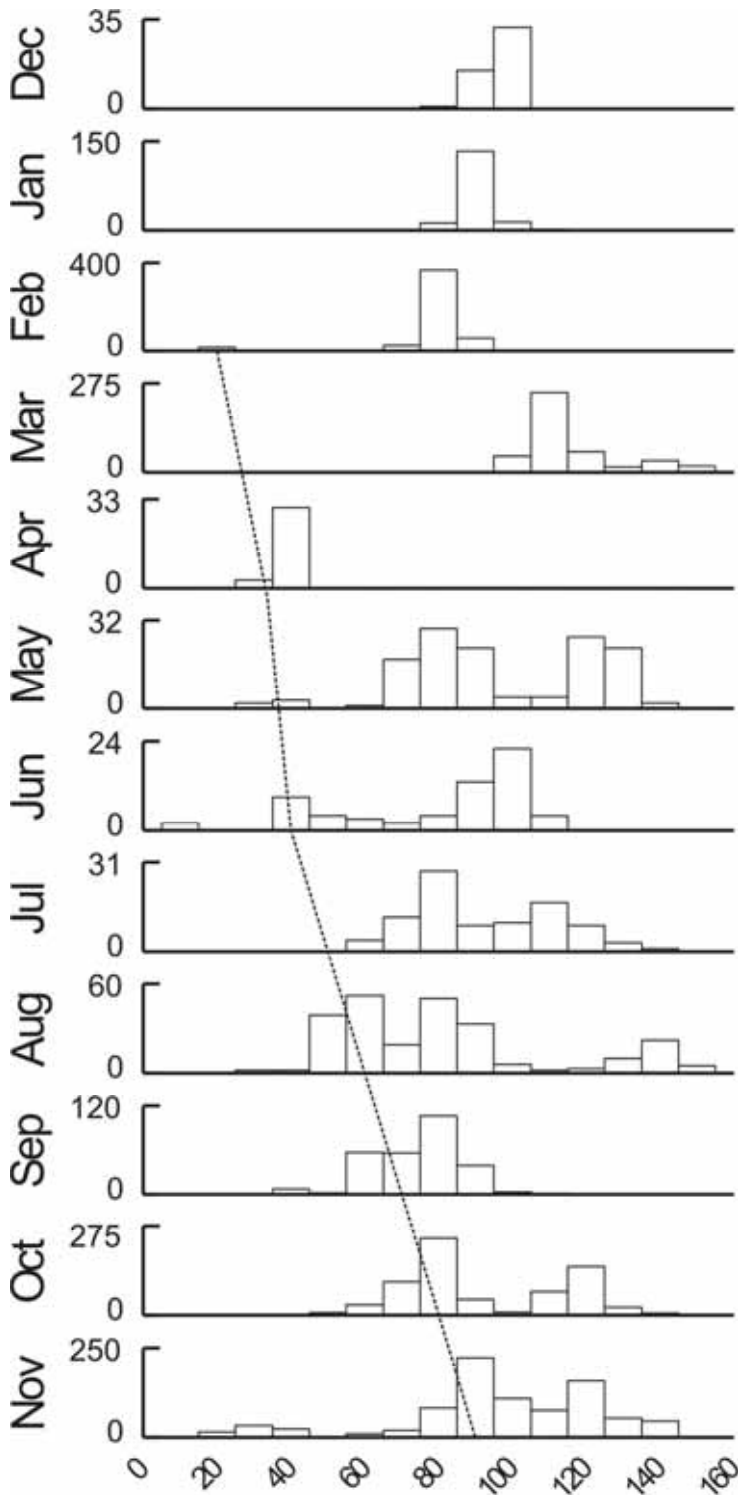


Figure 3.3 Length-frequency histograms combined from all regions for 2011. Dashed line connects modes thought to represent growing 0+ cohort.

Regional length/frequency comparisons

Length frequency distributions from the three SA regions were compared with data published for Port Phillip Bay (Blackburn 1950), Bass Strait (Hobday 1992) and Western Port Bay (Hoedt *et al.* 1995) (Fig. 3.4). Anchovy from the northern gulf areas (50 - 110 mm) were similar in size distribution to those from Port Phillip Bay (Blackburn 1950) (Fig. 3.4a). Frequencies of fish sampled in this region increased progressively from 50 to 90 mm in length due to the increasing retention rates of fish using the deployed mesh-size of the sampling gear. Fish from the southern gulf areas (70 - 140 mm) were similar in size to those from Western Port Bay (Hoedt *et al.* 1995) (Fig. 3.4b) and offshore fish (100 - 150 mm) were similar sizes to those collected in Bass Strait by Hobday (1992) (Fig. 3.4c).

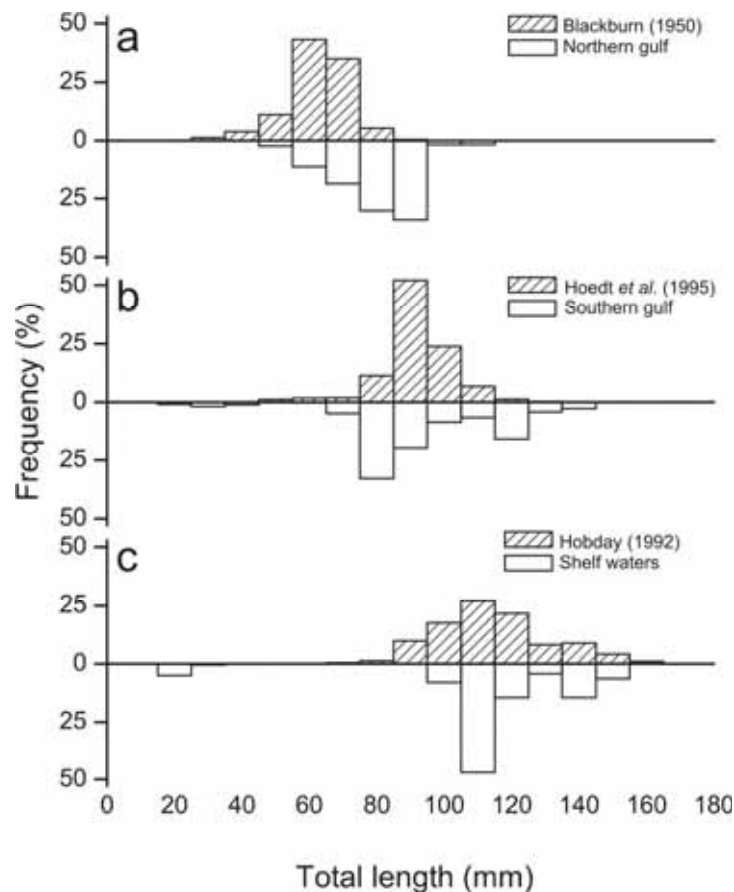


Figure 3.4 Comparisons of length/frequencies obtained for regions in this study with length/frequencies obtained in previous *Engraulis australis* studies.

Age and Growth Rates

Growth increments were clearly visible in sagittae from post-larval *E. australis*. Counts of growth increments were obtained from 108 larvae ranging from 13.0 to 45.4 mm TL (Fig. 3.5). The Laird-Gompertz function parameters were $a = 4.04$ mm and $b = 0.11$ and $c = 0.04$ ($r^2 = 0.74$) describing fast growth during the pre-metamorphosis stage.

Daily instantaneous growth rates for larvae below 30 mm TL ranged from a minimum of 0.63 mm day⁻¹ at 13.0 mm TL to a maximum of 0.75 mm day⁻¹ at approximately 25 mm TL (Fig. 3.5). At metamorphosis, daily growth rates had declined to 0.20 mm day⁻¹.

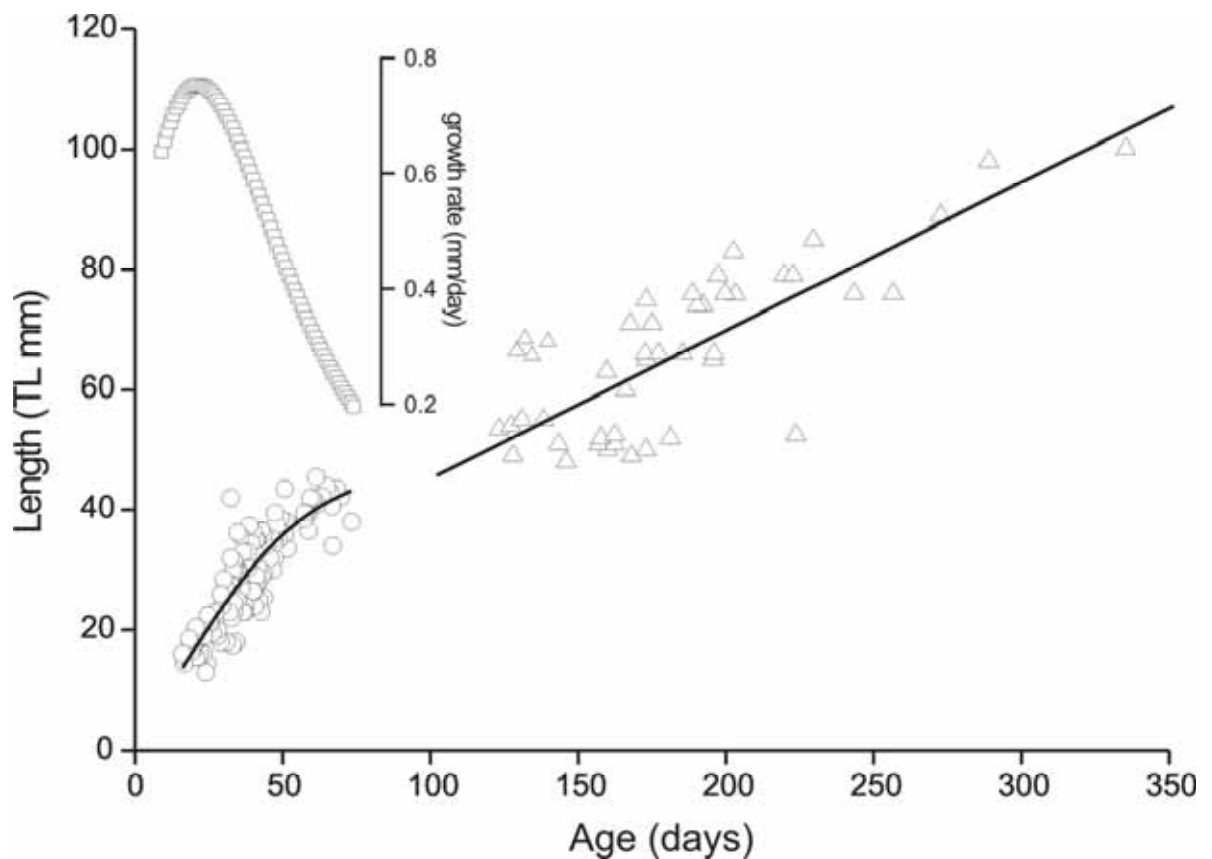


Figure 3.5 Growth curves for *Engraulis australis* fitted to larval data (circles) and juvenile/adult (young of year) data (triangles). Instantaneous daily larval growth rates are included (squares).

The growth of 46 anchovies from 48 to 100 mm is described by a linear regression (Fig. 3.5) $TL = 20.51 + 0.25Age_{days}$ ($r^2 = 0.67$). Extrapolation of this linear model results in a predicted length at age 1 or $L_{(1)}$ of approximately 110.5 mm with a mean growth rate of

0.25 mm day⁻¹ over the measured size range.

Fish between the ages of approximately 60 - 110 days (Fig. 3.5) were unable to be hand netted at the surface and fell below the size which was able to be captured by the gill nets.

A total of 426 adult anchovies were aged by counting opaque zones in whole otoliths. Anchovy aged 0 to 5 yrs were identified in the samples. Of these, 147 fish were identified as 0+ and were substituted in the model by the 108 larval fish to 45 mm TL which had been aged using daily growth increments in sectioned sagittae. The VBGF was fitted to these data resulting in parameter estimates of $L_{\infty} = 145$ mm and $k = 1.3$ and predicts an $L_{(1)}$ of 112.2 mm (Fig. 3.6).

An estimation of growth parameters using ELEFAN I produced values of 157.5 and 1.01 for L_{∞} and k respectively (Fig. 3.6). An analysis of co-variance (ANCOVA) taking the length (log-transformed) as a variable, the age as a co-variate and the estimation method as a factor (otolith-based or length-based) indicated there were no significant differences between growth patterns described by the otolith and length-based aging methods ($F = 0.01$, $P = 0.92$). Both models described higher growth rates than those described by Blackburn (1950) using perceived annuli in scales (Fig. 3.6).

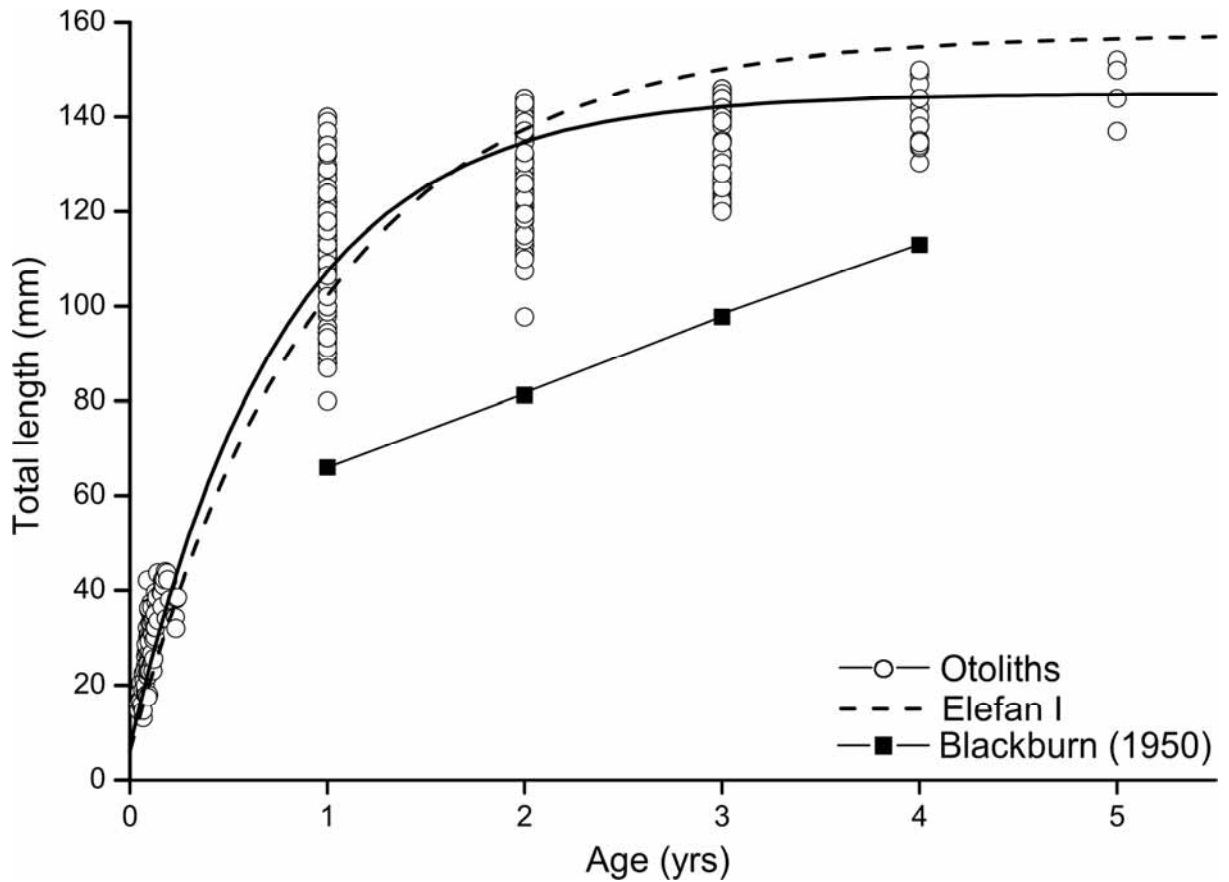


Figure 3.6 Von Bertalanffy growth function (VBGF) fitted to annual ages for *Engraulis australis* calculated from both direct otolith aging and ELEFAN. Blackburns (1950) age estimates from scales are included.

Length at maturity

During the spawning periods the observed reproductive stages increased progressively with size of fish ranging from exclusively immature at < 69 mm to exclusively mature >125 mm. The estimated L_{50} was 98.91 mm (Fig. 3.7) or less than 1 year of age.

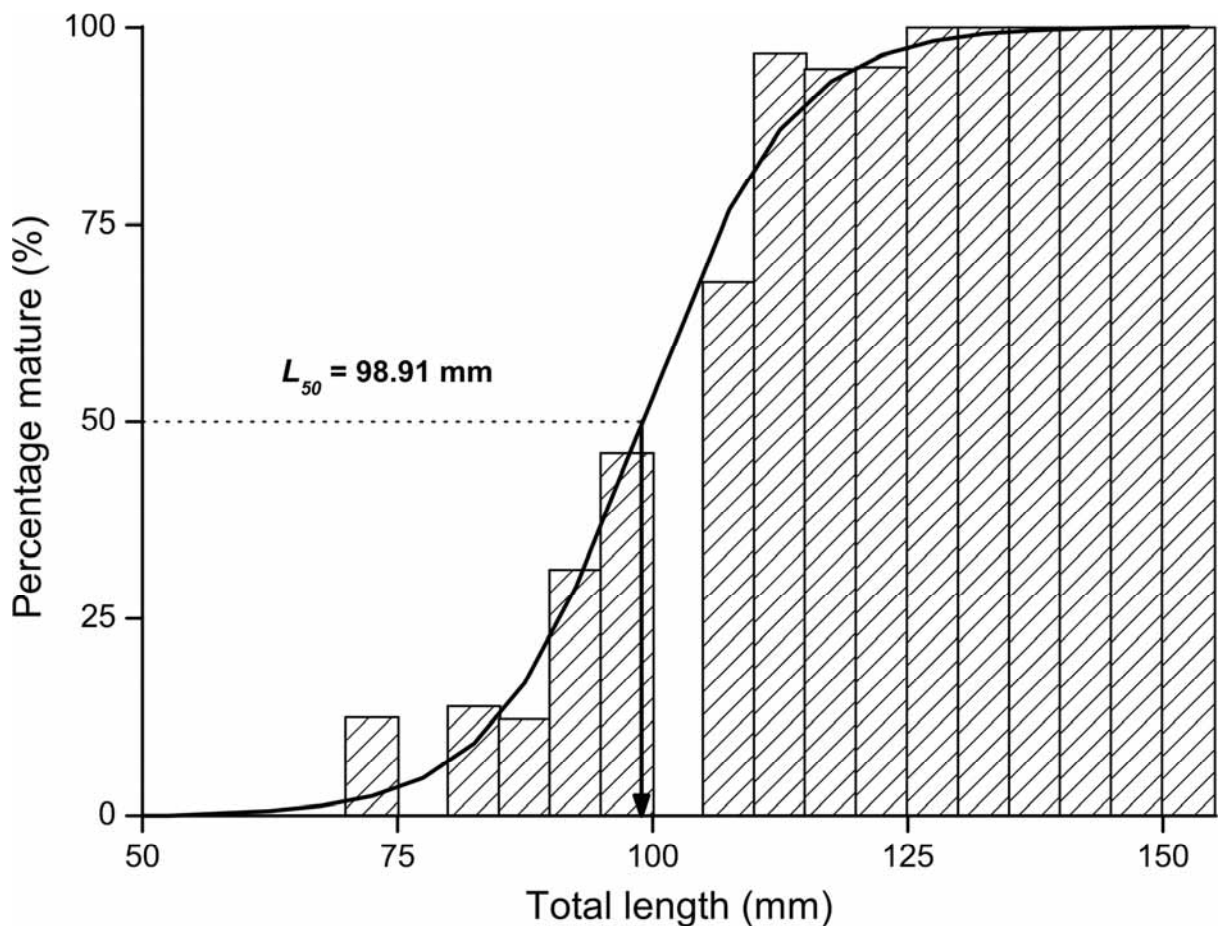


Figure 3.7 Percent frequency of mature anchovies sampled in South Australian waters during 2000. The logistic function was fitted to estimate L_{50} at first maturity.

Discussion

Direct aging by otolith increment analysis, corroborated by length-based growth models and visual analysis of modal length progressions, indicate that anchovies in South Australia grow much faster during their first year than estimated by Blackburn (1950) for Victoria. Whereas Blackburn (1950) suggested that *E. australis* reach 60 mm after 1 year we estimate a length of 110 mm at 1 year. While these results may reflect regional differences in growth it may also be possible that Blackburn's (1950) unvalidated scale-based estimates underestimated growth rates.

The von Bertalanffy growth parameters estimated for anchovy in the present study ($k = 1.3 \text{ year}^{-1}$) using length-based methods fell within the ranges of estimates for other

engraulid species. For example, Prosch (1986) used length-based methods to estimate k values from $0.9 - 1.1 \text{ year}^{-1}$ for *E. encrasicolus* (South Africa) for individual years between 1964 and 1983. Pauly and David (1981) used ELEFAN to estimate growth in *E. ringens* from Peru and obtained a k value of 0.7 year^{-1} . Beverton (1963) lists published k values for *E. encrasicolus*, *E. japonicus* and *E. mordax* of $1.0 - 1.8$, 1.6 and $0.4 - 0.5$ respectively.

Fish collected in the present study were aged up to 5 years by both otolith- and length-based methods, suggesting that South Australian anchovies may be one of the more long-lived *Engraulis* species. Previously, Spratt (1975) used annuli in otoliths to age northern anchovy *E. mordax* ($L_{\max} = 155 \text{ mm TL}$) up to 6 years and Bellido *et al.* (2000) suggested a 5 year lifespan for *E. encrasicolus* using length-based methods. However, the maximum ages estimated for *E. japonicus* ($L_{\max} = 150 \text{ mm TL}$) and *E. encrasicolus* ($L_{\max} = 150 - 200 \text{ mm TL}$) were 2.5 and 3 years respectively (Beverton 1963). Melo (1984) also estimated a maximum age of 3 years for *E. encrasicolus* off South West Africa with the Peruvian anchovy *E. ringens* having a lifespan of only 2 - 3 years (Longhurst and Pauly 1987).

Fish taken in the present study from the northern gulf were of similar lengths to those taken from inshore areas in other studies, ie. around 60-100 mm (Blackburn 1950; Hoedt and Dimmlich 1995). However, whereas Blackburn (1950) suggested that fish in Port Phillip Bay were between 2 - 3 years of age, we estimated fish in the northern gulf were no more than 1 year old. As indicated above, these differences could reflect real differences in growth rates due to regional variations, but could also reflect problems associated with scale-based age estimation.

Our results suggest that anchovy exhibits size and age-related distribution patterns in South Australian waters with small, young fish mainly inhabiting the northern gulfs, fish of mixed sizes and ages occurring in the southern gulf, and larger, older fish being found in shelf waters. No evidence was found to support the 'duo phase' life cycle described by Blackburn (1950) which proposed that larger fish returned to inshore areas in subsequent years to spawn. No anchovies above 110 mm (or 1 year of age) were

collected from the northern Spencer Gulf. Spawning fish at these lengths/ages were not caught in southern Spencer Gulf or shelf waters of the eastern Great Australian Bight (GAB). These observations are consistent with observations for other engraulid species, such as *E. mordax* (Curtis 2004) and *E. encrasicolus* (Barange *et al.* 1999), which tend to move offshore as they grow.

Dimmlich *et al.* (2004) identified the northern gulf as a centre of spawning activity for anchovy in South Australia. The relatively shallow and sheltered environment of the northern gulf is characterised by high annual fluctuations in temperature, with high temperatures in summer during spawning. Other species of anchovy, such as *E. encrasicolus* (Shelton and Hutchings 1990; Wilhelm *et al.* 2005) also spawn in warm waters with low levels of mixing (Wroblewski and Richman 1987; Robinson 2004). There is minimal exchange with lower gulf waters (Bullock 1975) and hence no spatial discontinuity between spawning ground and nursery area as exists with *E. encrasicolus* (Shelton and Hutchings 1981; Mullan *et al.* 2003). In this large area of the gulf (approximately 500 km²) the retention of larvae is maximised and the habitat is generally homogeneous during the extended spawning season providing a consistently favourable nursery for *E. australis*.

Southern Spencer Gulf is occupied by a range of age classes of anchovies, and may be more suitable than the northern gulfs for the survival of larvae to larger sizes (Dimmlich *et al.* 2004). These areas are characterised by temperature and salinity frontal zones which may aggregate the prey of larval and juvenile fish (Bruce and Short 1990; Hansen *et al.* 2001). It is unknown whether juvenile anchovies spawned in the northern gulf migrate to these prey-rich areas. However, migrations by larvae and maturing adults from spawning grounds to feeding areas have been recorded in *E. encrasicolus* in South Africa (Cruikshank 1990) and Europe (Basilone *et al.* 2004).

Anchovy in shelf waters of South Australia are predominantly greater than 3 years old. The upwelling conditions in these waters appear to be favourable for anchovy spawning (Ward *et al.* 2001; Dimmlich *et al.* 2004), presumably because the high concentrations of planktonic food required by first feeding anchovy larvae can be found in the upper

water column (Blaxter and Hunter 1982). However the eggs and larvae spawned in these areas may be subject to the fluctuations in conditions common to all boundary current systems. Anchovies also appear to compete unsuccessfully with sardines in these areas (Ward *et al.* 2001; Dimmlich *et al.* 2004).

It appears that anchovy in South Australia, through their tolerance of a broad range of conditions, are able to exploit widely differing environments during the summer–autumn spawning season. In contrast, the Australian sardine occurs mainly in the southern gulf and upwelling regions and can-not utilise the relatively benign environment found in the warm and saline waters of the northern Spencer Gulf. The range of adaptive strategies that anchovy utilise in various boundary current systems is only recently being elucidated (Bertrand *et al.* 2004). Owen *et al.* (1989) suggested that different components of a single anchovy population may spawn in different areas with varying associated conditions during a single spawning season. The present study suggests that for *E. australis* in South Australia these population components are strongly defined by age. A similar mechanism may be occurring in other Australian waters where age gradients have been described (Blackburn 1950; Hobday 1992; Hoedt *et al.* 1995) but further, more comprehensive, ageing of anchovies in these locations is required to confirm this hypothesis.

Additional otolith-based investigations of age and growth of anchovy in Victorian waters are also needed to determine if the growth rates in that region (Blackburn 1950) differ significantly from those measured in the present study.

Chapter 4

SPAWNING DYNAMICS AND BIOMASS ESTIMATES OF AN ANCHOVY (ENGRAULIS AUSTRALIS) POPULATION IN CONTRASTING GULF AND SHELF ENVIRONMENTS.

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Statement of Authorship

Spawning dynamics and biomass estimates of an anchovy (*Engraulis australis*) population in contrasting gulf and shelf environments.

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Conducted fieldwork, performed analysis on all samples, interpreted data, primary and corresponding author of paper.

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Abstract

The spawning biomass of Australian anchovy (*Engraulis australis*) in gulf and shelf waters of South Australia was compared. Egg densities were high in gulf waters which were only inhabited by small young (<1 yr old), anchovies that spawned relatively small batches of eggs (~ 850) approximately every 3 days. In shelf waters, where larger, older anchovies compete with sardine (*Sardinops sagax*), lower egg densities occurred despite individuals producing much larger batches of eggs (~ 15 500) approximately every 7 days. Females were more abundant than males in samples from both gulf and shelf waters. The spawning biomass of anchovy in shelf waters was over 101 000 tonnes, whereas the estimate for gulf waters was approximately 25 000 tonnes. However, due to the differences in mean size of the spawning females, approximately 6 billion anchovies were present in each region. Gulf waters appear to provide Australian anchovy with a refuge from competition with sardine, from which the population can rapidly expand when conditions become favourable offshore, particularly when the sardine abundance is reduced.

Key words: daily egg production; anchovy; clupeidae; biomass; spawning; fecundity

Introduction

Clupeoid fishes are able to utilise a range of flexible behaviours to maximise recruitment in the dynamic pelagic environments typical of productive coastal upwelling zones (Bertrand *et al.* 2004; Robinson, 2004). These key prey species usually comprise a high proportion of the total biomass in such ecosystems (eg. e.g. Schwartzlose *et al.* 1999; Ward *et al.* 2006). Anchovies (*Engraulis* spp.) are common in many upwelling systems and often display flexible reproductive strategies (Shelton & Hutchings, 1981; Palomera, 1992; Hugget *et al.* 2003; Wilhelm *et al.* 2005). Owen *et al.* (1989) proposed that spatially separated components of some anchovy populations do not spawn indiscriminately but tend to spawn under conditions and at levels that yield optimal survival probabilities for larvae and juveniles.

In South Australia, extensive ichthyoplankton surveys have been carried out since 1995

to support annual assessments of sardine (*Sardinops sagax* Jenyns) stocks. These surveys also indicated that a sizeable stock of Australian anchovy (*E. australis* White) was co-occurring in shelf waters of South Australia. Spawning areas and egg densities for anchovies sometimes exceeded those recorded for sardines, most notably during years following mass species-specific mortality events which drastically depleted sardine stocks in coastal waters of southern Australia (Ward *et al.* 2001a). Ichthyoplankton surveys carried out during the 1980s provided additional evidence of even higher levels of anchovy spawning activity in the northern regions of Spencer Gulf and Gulf St Vincent (Dimmlich *et al.* 2004).

The gulf and shelf regions of South Australia are vastly different environments. During the summer anchovy spawning period, Spencer Gulf and Gulf St Vincent are expansive inverse estuaries with low to moderate wave energy environments and mean depths of about 20 m (IMCRA, 1998). Water temperatures up to 30°C and salinities up to 50 are recorded in the shallow (<10 m) northern reaches (Bruce & Short, 1990; IMCRA, 1998). Few rivers feed into the gulfs, and there are few other sources of nutrient enrichment so levels of primary and secondary production are low. In contrast to the gulfs, shelf waters of the eastern Great Australian Bight are moderate to high wave energy environments in which pelagic production is enhanced throughout summer and autumn by upwelling of cool nutrient rich water (Kampf *et al.* 2004; McClatchie *et al.* 2006; Ward *et al.* 2006). Gulf and shelf waters are effectively delineated during this period by thermal and saline frontal systems which form at the entrances to the gulfs (Bruce & Short, 1990).

These two very different regions are utilised as spawning and nursery areas by two distinct components of the single South Australian population of *E. australis*. The relatively protected inshore gulf waters are occupied exclusively by fish less than 1 year old (Dimmlich & Ward, 2006) and support the highest egg densities of anchovies in South Australian waters (Dimmlich *et al.* 2004). In contrast, egg densities are generally lower in shelf waters, where dispersal by upwelling and wind driven transport processes can reduce intraspecific predation (Funamoto & Aoki, 2002) and enhance survivability to later stages (Dimmlich *et al.* 2004) with the trade off of potential

transport into unfavourable habitats (Economou, 1991).

The relative importance of gulf and shelf waters of South Australia as spawning and nursery areas for Australian anchovy, and differences in the anchovy age composition between these two regions have been investigated (e.g. Dimmlich *et al.* 2004; Dimmlich & Ward, 2006). However, the reproductive patterns and spawning biomass of the anchovy in these two regions is currently unknown.

Estimates of spawning stock biomass (SSB) estimates of sardine in South Australia have been obtained annually for over a decade using the daily egg production method (DEPM). This ichthyoplankton-based method is considered a robust fishery-independent method of estimating SSB for small pelagic fishes such as anchovy and sardine (Hunter & Lo, 1997) and has been used for many years off California to estimate stock levels and recommend management levels of northern anchovy, *E. mordax* (Picquelle & Hewitt, 1983, 1984; Bindman, 1986). Elsewhere it has also been applied to the Peruvian anchovy, *E. ringens* (Santander *et al.* 1984; Cubillos *et al.* 2007), southern Benguela anchovy, *E. encrasicolus* (Armstrong *et al.* 1988; Shelton *et al.* 1993) and European anchovy *E. encrasicolus* in the Gulf of Biscay (Santiago & Sanz, 1992; Motos & Santiago, 1990), Catalan Sea, Gulf of Lions and Ligurian-North Tyrrhenian Seas (Palomera & Perterra, 1993; García *et al.* 1995), Black sea (Arkhipov *et al.* 1991) and Aegean sea (Tsimenides *et al.* 1995).

The egg surveys conducted in South Australian shelf waters from 1995 to 1999 for sardine biomass determination also enabled an assessment of the spatial and temporal distribution of the egg stages and the delimitation of the spawning areas of anchovies (Smith & Hewitt, 1985) in offshore waters. However as the northern gulf areas lay outside the range of sardines they were not included in the annual DEPM survey. Additionally, the apparent stratification by age of the anchovy spawning areas presents further considerations. Three of the parameters needed for the DEPM determination are mean female body weight, mean batch fecundity and spawning frequency. Each of these parameters is likely to change between the first spawning by smaller fish of less than one year of age in the northern gulfs and later offshore spawning by older fish

(Dimmlich & Ward, 2006). These parameters may also differ considerably between regions due to variations in temperature and productivity (Funamoto & Aoki, 2002; Somarakis *et al.* 2002; Takasuka *et al.* 2005; Stratoudakis *et al.* 2007), resulting in recommendations for further inshore-offshore comparison of the spawning ecology of small pelagic fish subject to DEP methodologies (Takasuka *et al.* 2005).

The present study represents the first biomass assessment of the anchovy, *Engraulis australis*. The objective was to assess independently the separate spawning populations in the gulf and shelf regions of South Australia. This was achieved by extending the existing sardine ichthyoplankton surveys in 2000 into the northern gulfs to obtain samples of adult anchovies and eggs in order to 1) determine the distribution and abundance of anchovy eggs, 2) estimate the spawning area (A) and mean daily rate of size-specific egg production (P) in gulf and shelf areas, 3) estimate the adult reproductive parameters (mean female weight, sex ratio, fecundity and spawning fraction), and 4) use these parameters to estimate the separate spawning stock biomass of the anchovy in both the northern gulf and shelf waters by the daily egg production model.

Methods

In order to determine the extent of spawning activity identified by the 1986-1999 surveys, sampling sites were located throughout gulf and shelf waters of South Australia during February to March, 2000 (Fig. 4.1). Shelf transects were aligned perpendicular to the coast and gulf transects were aligned east-west. A total of 290 samples was collected using paired CalVET nets (0.225 m diameter, 300 μm mesh), deployed vertically at shelf stations to within 10m of the seabed prior to retrieval. Wire lengths were digitally recorded during deployment. In gulf waters, which were too shallow to accommodate vertical tows, an identical CalVET net was deployed and retrieved obliquely from smaller vessels (Fletcher & Tregonning, 1992). A total of 30 double oblique tows were conducted, averaging 5-10 minutes at a towing speed of approximately 1.5 ms^{-1} . These nets were towed to within several metres of the bottom and returned to the surface in a step-wise sequence designed to sample the water column evenly. Previous comparative

studies between vertical and oblique tows have not found any significant between-gear differences in the mean abundance of anchovy eggs (Somarakis *et al.* 2004).

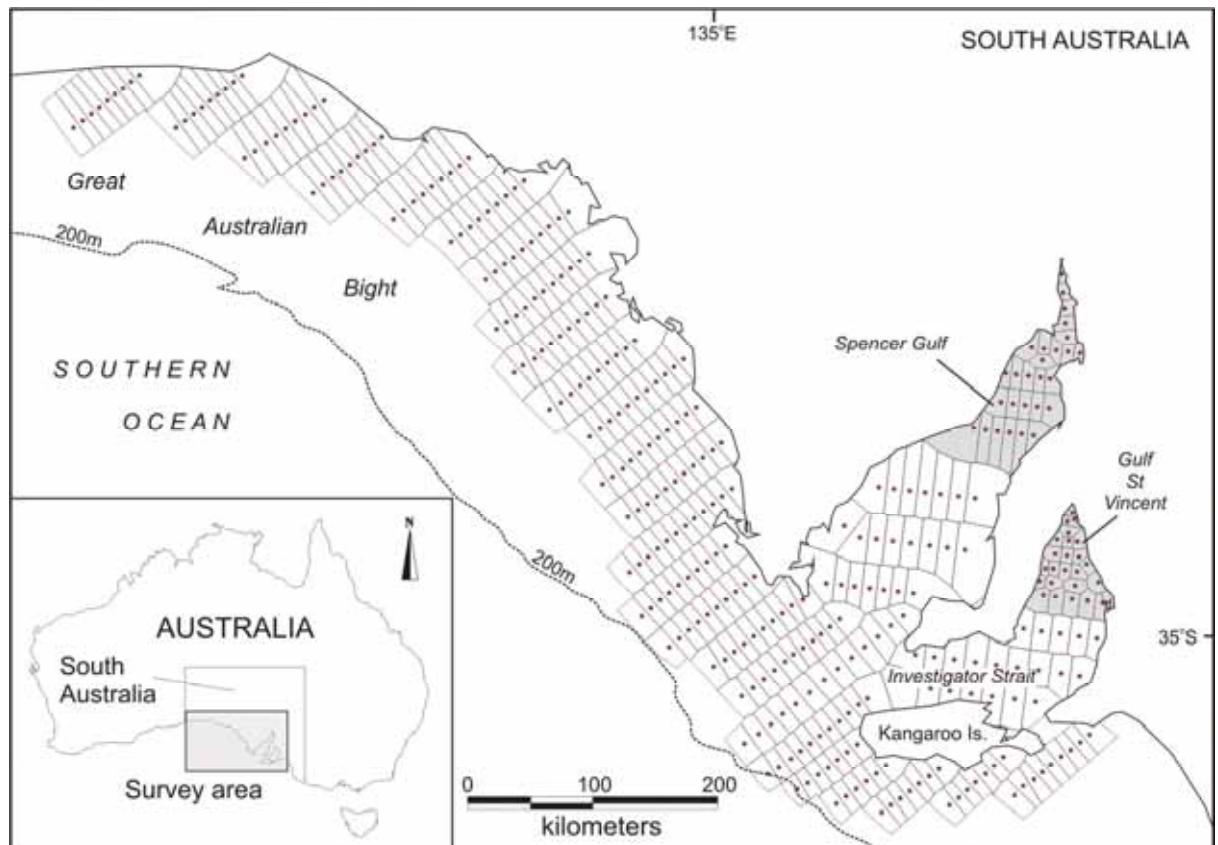


Figure 4.1 Locality map showing ichthyoplankton stations and sites from which adult fish were sampled. Polygons used for area estimates are shown for each station. Shaded area represents the northern gulf stratum.

Known wire-lengths provided the distance travelled during vertical hauls. The distance travelled by each net during the oblique tows was estimated using net-mounted flowmeters which were calibrated using the known wire-lengths obtained from the vertical tows. The volume of water filtered was calculated by multiplying the distance towed by the surface area of the net. Both methods sampled the extent of the water column. Fish larvae and egg samples were preserved in 5% formaldehyde seawater solution. These samples were later rinsed with freshwater and the identity of all clupeoid eggs and larvae determined under microscopic examination and counted. The numbers of anchovy eggs caught per cubic metre of water filtered (density) was

converted to mean numbers per m² of sea surface area using data on total volume filtered and the distance and depth towed.

The survey area was divided into a series of contiguous polygons with each sampling site as the centroid. Natural neighbours were built around each data point using Delaunay triangulation (Vertical Mapper®, Troy, NY, U.S.A.), generating a network of Thiessen polygons (Fig. 4.1). The seaward hull boundary defining the resulting Voronoi diagram is an artificial constraint to prevent the application of the interpolation algorithms beyond available data limits and is not mathematically defined. The coastline was used to define the landward extent of the polygons. The area of each polygon was determined using geographical information system (GIS) software (Mapinfo®, Troy, NY, U.S.A.). The spawning area (A) was defined as the total area of grids where live, stage 1-8 (0-25 hr old) anchovy eggs were found. Embedded polygons, where zero egg counts were recorded, were not included in the area calculations. Using these methods the spawning areas for gulf and shelf areas were estimated. The areas defined in this study as 'gulf' and 'shelf' were delimited based on the results of the current egg survey and on previous ageing studies of anchovy (Dimmlich *et al.* 2004).

Mean daily egg production (P_0) was estimated using the exponential egg mortality (exponential decay) model modified from Picquelle and Stauffer (1985) which has the form

$$P_j = P_0^{-Zy_j} \quad \text{Eq. 2}$$

Where P_j is density of eggs (per unit area) in age category j , P_0 is the daily egg production per unit area, Z is the instantaneous rate of egg mortality and y_j is the mean age of eggs in the j -th age class. The mortality model was estimated using eggs grouped into ½ day age categories (Lo, 1985). The model was fitted using weighted (by polygon area) non-linear least squares regression provided by the Solver function of Microsoft Excel™ (Microsoft, Redmond, California, U.S.A.).

Eggs were assigned ages using the continuous form of the equation derived from incubation experiments on *E. mordax* over a temperature range of 10 to 22 °C (Lo,

1985) and extrapolated for the higher temperatures recorded in the current study,

$$Y(t, i) = a^{(bt+ci)} t^d \quad \text{Eq. 3}$$

Where $Y(t, i)$ is the average age (in hours) of an egg from the i -th stage at temperature t ; a , b , c , and d are parameters obtained by egg development experiments at different temperatures. In the absence of equivalent data for *E. australis* we used data calibrated for European and South African anchovy *E. encrasicolus* (Melià *et al.* 2002) which occurs at similar sizes and latitudes to the southern hemisphere *E. australis*.

There was insufficient temporal resolution for egg data from the gulf areas which resulted in no significant slope of the egg mortality curve. This is due in part to a combination of a relatively low number of stations (Fig. 4.2(a)) and high incubation temperatures (Fig. 4.2(b)) which may significantly reduce the duration of egg stages in the water column. To overcome this lack of data, both eggs and yolk-sac larvae were included in the mortality curves, in the assumption that there was a similar mortality rate (Hunter & Lo, 1997; Somarakis *et al.* 2002).

During the egg survey the research vessel was anchored in the evenings where schools of baitfish were detected using a dual frequency echo sounder (Furuno: 60 and 180 KHz). Schooling baitfish were attracted to the vessel using submerged incandescent lights and samples were collected using a gillnet comprising of three panels, each with a different multifilament nylon mesh size (Double Diamond: 210/4 ply meshes – 25, 28 and 32mm). The ovaries were removed from the hydrated females and were immediately fixed in 5% buffered formaldehyde for later histological analysis. A similar technique using identical gillnets was employed in gulf regions, however in the shallower waters it was necessary to use a smaller vessel with less capable electronic aids which limited the ability to search for spawning adults.

Ovaries were weighed (M_G) to the nearest 0.1 mg and cut longitudinally, and the oocytes were washed from the ovary into a sample of water to 200 ml total volume. Three 6 ml subsamples were then examined under a binocular microscope using transmitted light and hydrated oocytes counted. Estimates of batch fecundity (F) were obtained by

extrapolating these counts to the full 200 ml sample volume and combined weight of both ovaries.

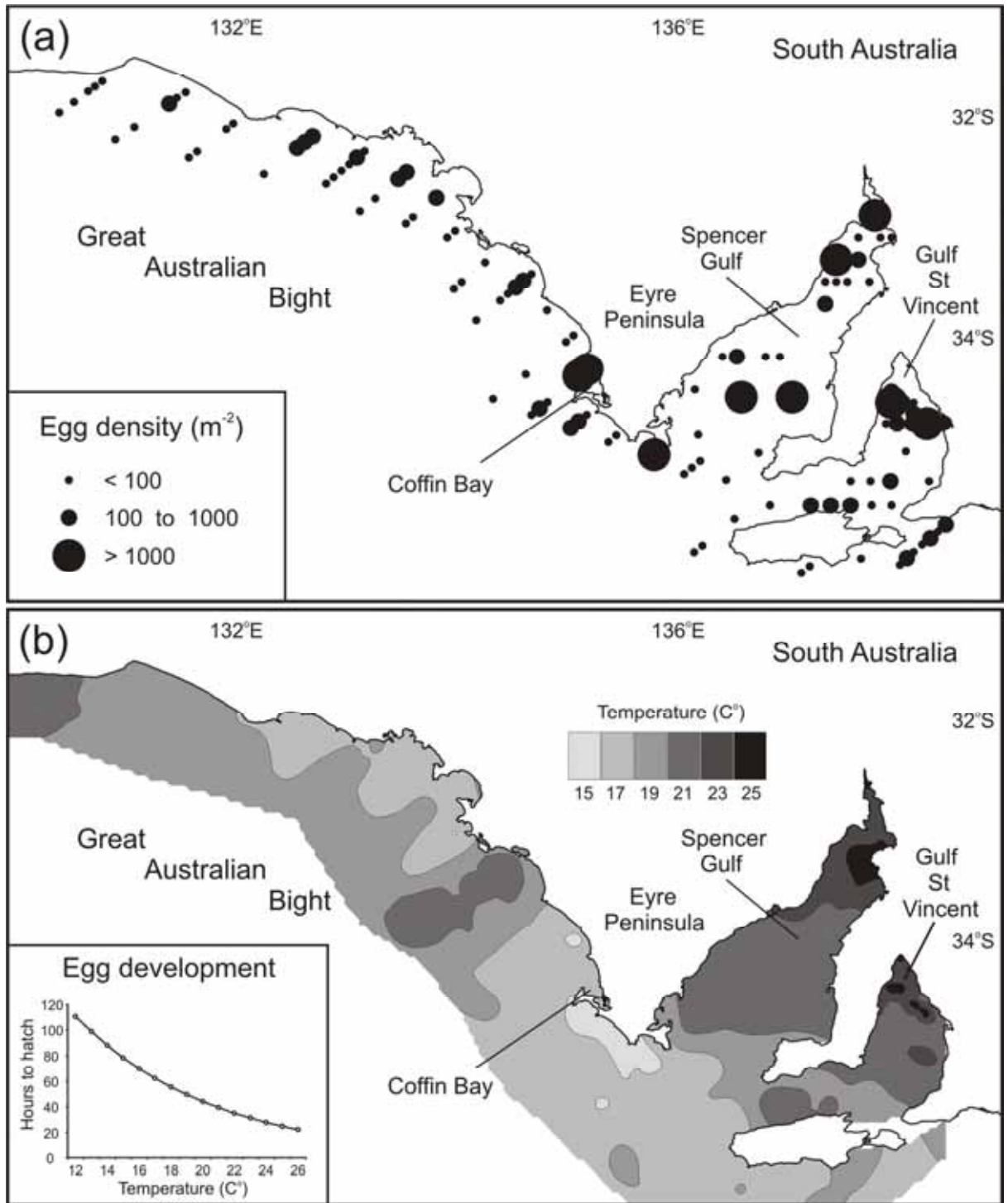


Figure 4.2 Anchovy egg densities (a) and sea surface temperatures (b) for 2000. Inset on (b) illustrates

development rates for anchovy eggs over a range of temperatures for *E. encrasicolus* (from Melià, 2002).

Mature females from each sample were weighed (M) to the nearest 0.01 g. The mean weight of mature females in the population (W) was calculated for both shelf and gulf regions from the average of sample means weighted by sample size. The sex ratios were calculated from the weight of mature females divided by the sum of the total weight of mature females and mature males. Mean sex ratios (R) ratios of anchovy populations in the shelf and gulf regions were calculated from the average of sample means weighted by sample size.

Ovaries of mature females were fixed in formalin, embedded in paraffin wax, sectioned at 7 μ m and stained with haematoxylin and eosin. Approximately four sections from each ovary were examined to determine the presence/absence of post-ovulatory follicles (POFs) which were aged according to the method of Hunter & Goldberg (1980) and Hunter & Macewicz (1985). The spawning fraction of each sample was estimated as the mean proportion of females with day-0 POFs (d_0 ; Fig. 4.3(a)), day-1 POFs (d_1 ; Fig. 4.3(b)) and day-2 POFs (d_2 ; Fig. 4.3(c)). The mean spawning fraction of the population (S) was then calculated from the average of sample means weighted by proportional sample size.

$$S = \left[\overline{S_i} * \frac{n_i}{N} \right] \quad \text{Eq. 4}$$

where n is the number of fish in each sample, N is the total number of fish collected in all samples and $\overline{S_i}$ is the mean spawning fraction of each sample calculated from the equation:

$$\overline{S_i} = \frac{[(d_0 + d_1 + d_2 \text{POFs})/3]}{n_i} \quad \text{Eq. 5}$$

where d_0 , d_1 and d_2 POFs are the number of mature female sardines with POFs in each sample and n_i is the total number of female sardines within a sample.

The spawning stock biomass was estimated according to the model described by Parker (1980) and subsequently modified by Stauffer and Picquelle (1980):

$$B = \frac{P \cdot A \cdot W}{R \cdot F \cdot S} \quad \text{Eq. 1}$$

Where B is the spawning stock biomass in metric tonnes, P is the daily egg production of number of eggs per unit area of sea surface (eggs/m²/d), A the total spawning area (in sampling units, km²), W is the average weight of mature females (g), R is the sex ratio (fraction of mature females by weight), F the batch fecundity (mean number of eggs per mature female per spawning), and S the fraction of mature females spawning per day (a measure of spawning frequency).

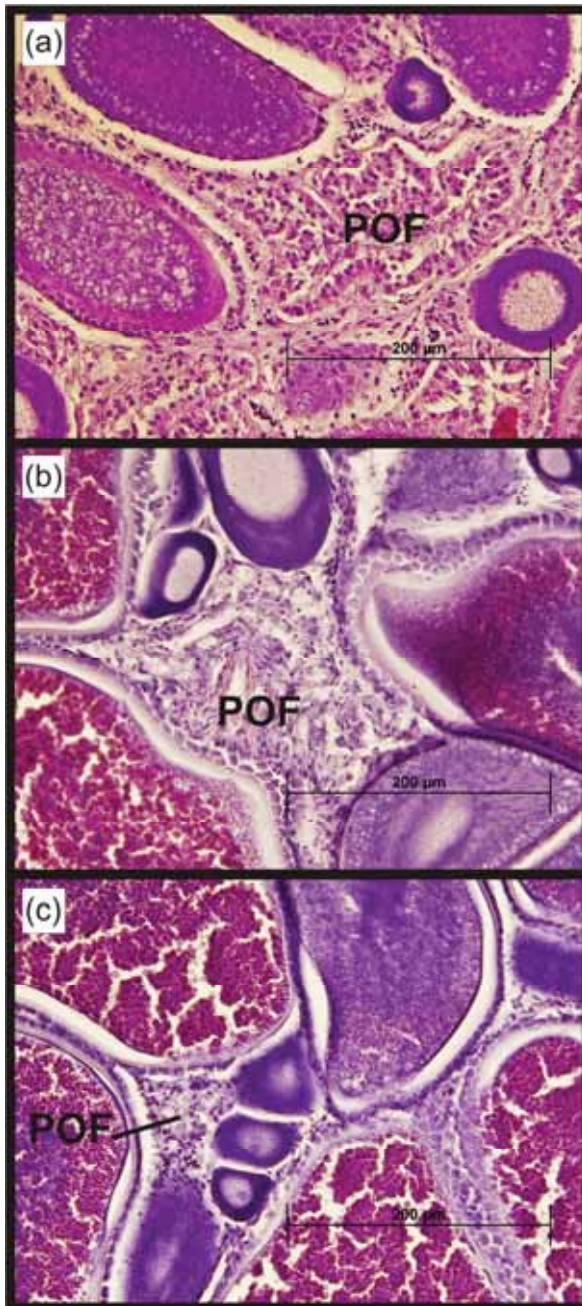


Figure 4.3 Anchovy (*Engraulis australis*) post ovulatory follicle (POF) stages used in identifying daily cohorts. (a) Day-0 POF remains a discernible convoluted shape with the individual cells of the granulosa cell layer distinct and generally arranged linearly; (b) Day-1 POF is much less convoluted and presents a more disorderly arrangement of the cells of the granulosa layer; (c) Day-2 POF is greatly reduced in size and at an advanced stage of degeneration, with the granulosa and theca generally indistinguishable and little evidence of cellular organisation.

The 95% confidence intervals for each independent adult population parameter were estimated using the nonparametric naïve bootstrap method (Smith, 1997) which

provides acceptable results in small samples (Jackson & Cheng, 2001).

Results

A total of 128 700 km² was surveyed in gulf and shelf waters of South Australia and, for the year 2000, the distribution of anchovy eggs within the survey area is shown in Figure 4.2(a). Spawning occurred over the entire shelf region with higher densities recorded near the upwelling areas off Coffin Bay and southern Eyre Peninsula. Densities were generally higher at the inshore shelf stations than the outer shelf stations. The highest egg densities were recorded in the northern gulfs. High densities were also recorded in the southern Spencer Gulf in the vicinity of the frontal zones. Spawning took place over a total of 44 618 km² of the shelf, approximately nine times greater than the 4 898 km² spawning area contained within the gulf (Table I).

Table I. Summary of DEPM parameters and spawning biomass estimates for *E. australis* in the gulf and shelf regions of South Australia.

Parameter	Gulf	Shelf
Total area surveyed (km ²)	9 561	119 150
Area of spawning (A; km ²)	4 898	44 618
Daily egg production (P; eggs/m ² /d)	217.69 (95% CI, 165.05-321.12)	197.97 (95% CI, 138.65-305.75)
Average female Wt (W; g)	4.22 (95% CI, 3.62 – 4.81)	16.06 (95% CI, 13.65 – 19.91)
Batch fecundity (F)	855 (95% CI, 762 - 1052)	15572 (95% CI, 13900 - 16462)
Sex ratio (R; F:M)	0.61 (95% CI, 0.56 – 0.71)	0.56 (95% CI, 0.52 – 0.59)
Spawning fraction (S)	0.34 (N/A)	0.16 (95% CI, 0.14 – 0.21)
Biomass (B; tonnes)	25 374 (95% CI, 21 118 – 30 934*)	101 522 (95% CI, 53 719 – 173 690)

* Confidence intervals for gulf spawning biomass (B_{gulf}) estimated using fixed spawning fraction (S_{gulf})

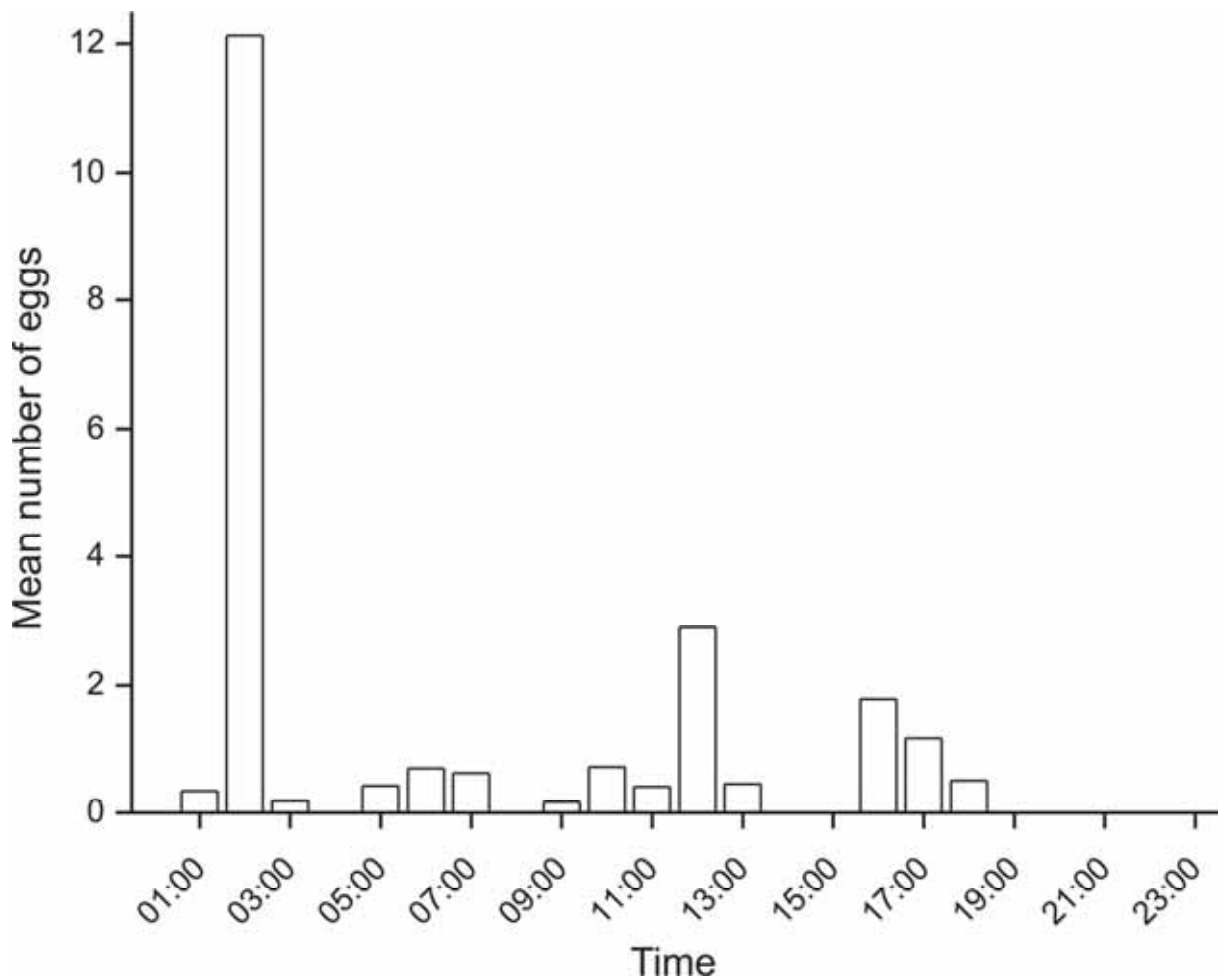


Figure 4.4 Mean numbers of anchovy Stage I eggs per station during a 24 hour period.

A wide temperature range was recorded over the survey area with cooler upwelling waters of 15°C off the southern Eyre Peninsula and warmer temperatures of over 25°C in the northern gulfs (Fig. 4.2(b)) characterising the two primary thermal regimes found in the region. In 2000 spawning took place throughout the temperature ranges recorded, with the highest concentrations of eggs recorded in areas near each of the temperature extremes (Fig. 4.2(a)).

The spawning time within the 24 period was determined from the occurrence of stage I eggs. These peaked at 0200 hours (Fig. 4.4) indicating that maximal spawning took place between 0000 and 0100 hours. Some low-level spawning activity occurs at all times of day and night as indicated by the presence of early stage eggs outside peak

spawning time.

Daily egg production was estimated for the areas in shelf and gulf waters where eggs were present. Due to the absence of final-stage eggs, yolk sac larvae were used in addition to eggs for the gulf areas to 'anchor' the end of the mortality curves. The daily egg production (P) was similar in both shelf and gulf regions (Fig. 4.5) ($P = 197.97$ eggs m^{-2} and 217.69 eggs m^{-2} respectively).

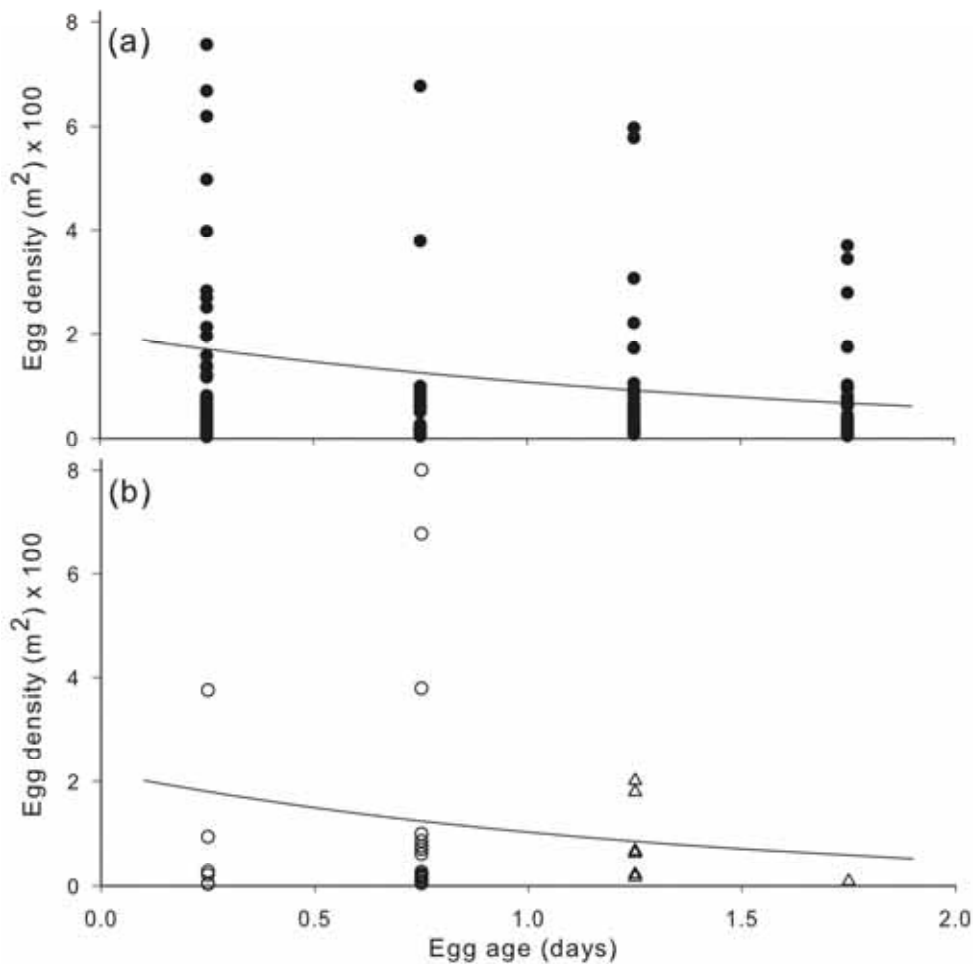


Figure 4.5 Egg densities are shown against egg ages (days) for shelf (a) and gulf (b) anchovies. Points representing yolk-sac larvae used in the gulf regions are identified by open triangles. Regression curves fitted to these data are shown for both shelf ($y = 199.97e^{-0.62x}$) and gulf anchovies ($y = 217.69e^{-0.75x}$).

Batch fecundities were derived from estimates on 33 fish from the gulfs and 66 fish from the shelf (Fig. 4.6). The relationships between gonad free weight ($M - M_G$) and fecundity (F) were described by the equations $F = 780.79(M - M_G) + 390.17$ and $F = 188.02(M - M_G) + 346.42$ for shelf and gulf anchovies respectively (Fig. 4.6a). Fecundity was linearly related to ovary weight (M_G) throughout the size range of anchovies sampled and was described by the equation $F = 4186.8M_G + 384.86$ (Fig. 4.6b). Mean batch fecundities for gulf and shelf waters were 855 and 15 572 oocytes respectively.

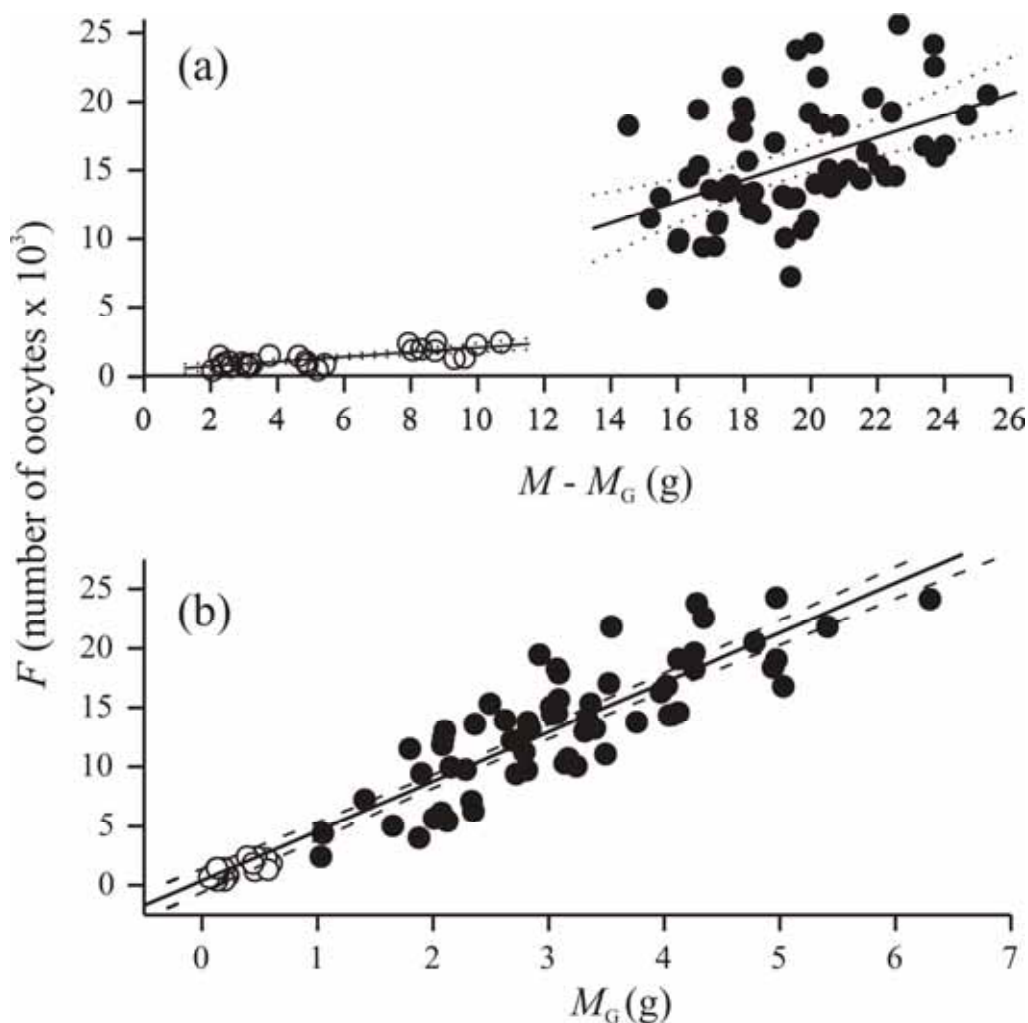


Figure 4.6 Regressions of batch fecundity (F) on gonad free female body weight (a) and gonad weight (b). Filled circles: Shelf. Open circles: northern gulfs.

The mean values (and associated 95% confidence intervals) for female weight (W), sex ratio (R), batch fecundity (F) and spawning fraction (S) parameters are shown in Table

I. Female weight, sex ratio and spawning fractions were 4.22 g, 0.61 and 0.34 respectively for gulf waters and 16.06 g, 0.56 and 0.16 respectively for shelf waters. Methods which were successful in sampling older anchovies in shelf waters were less successful in gulf waters due to differences in schooling behaviour by spawning fish and consequently only a single sample of 248 fish was sampled which was insufficient for estimation of confidence intervals for spawning fraction in the gulfs. Five samples totalling 152 fish were obtained from shelf waters.

In 2000 the estimated biomass of anchovy was approximately 101 500 tonnes for shelf waters and approximately 25 400 tonnes for the gulf regions. The total combined biomass for *E. australis* in South Australian waters during the 2000 spawning season was over 126 000 tonnes.

Discussion

This study estimates the DEPM parameters for the Australian anchovy, *E. australis* and provides the first examination of age- and region-specific differences in these parameters for an *Engraulis* species. Estimates of average female weight, batch fecundity and spawning fraction were markedly different between the two areas surveyed with much smaller and younger fish in the gulfs producing far smaller batches of eggs but at a higher frequency. This is perhaps due to a combination of ontogenetic and environmental factors. Minor differences in sex ratio between the two populations were also observed. Despite these differences, egg production for the two regions was similar. This results in a relatively high biomass estimate for the northern gulfs given the smaller area available for spawning compared to the expansive shelf waters.

The mean batch fecundity for offshore *E. australis* (15 572) lies at the mid to high end of the ranges reported for other engraulids. Batch fecundities for *E. encrasicolus* ranged from 5 627 to 9 045 in South African waters (Shelton *et al.* 1993) and to 15 783 in Europe (Somarakis *et al.* 2002; Somarakis *et al.* 2004). Similarly, batch fecundities for Peruvian anchovy (*E. ringens*) reached up to 8 497 (Cubillos *et al.* 2007) and for offshore Pacific anchovy (*E. japonicus*) off Japan and Korea were up to 19 528 (Takasuka *et al.* 2005; Funamoto & Aoki, 2002) and 15 316 (Kim & Lo, 2001), respectively. In contrast to

these estimates the mean batch fecundity for the smaller *E. australis* (~ 100 mm total length, L_T) occurring in the gulfs of South Australia was much lower (855). There are few studies on anchovies or other fish species of similar body mass. However Korean *E. japonicus* at lengths of 80 and 90 mm (fork length, L_F) exhibited similar mean batch fecundities of 485 and 1003 respectively (Kim & Lo, 2001). The large difference in fecundity between the gulf and shelf anchovies is likely a function of the size difference in spawning females in the two regions. Anchovies in South Australia attain their maximum adult growth rates between the first and second years (Dimmlich *et al.* 2006) and by their second spawning season have almost attained maximum size with commensurately larger and more productive gonads.

The fraction of spawning females in shelf waters (0.16 or a period of approximately one week between spawning events) was approximately half that of gulf anchovies (0.34 or a period with about a three day interval between spawning events). However, both estimates fall within ranges reported for other related species. For example, the spawning fraction of *E. encrasicolus* in Europe ranged from 0.06 to 0.36 (Somarakis *et al.* 2004; Motos, 1996) and in South Africa from 0.06 to 0.19 (Shelton *et al.* 1993; Melo, 1994). In several studies smaller and younger fish have been found to have lower spawning fractions with spawning fraction seeming to be dependent on female size (Claramunt *et al.* 2007). Cubillos *et al.* (2007) reported a spawning fraction of 0.15 for smaller *E. ringens* (equivalent in size to those in the northern gulf regions in SA) occurring in one part of the region surveyed studied and a lower spawning fraction of 0.07 for larger fish in a different spawning stratum. Although the estimates from the latter study were lower, the ratio between the two values was similar to the current study. A comparable relationship to *E. australis* and *E. ringens* was also found in *E. japonicus* with a spawning fraction of 0.20 for larger fish aged over 2 years which was almost half that (0.37) for the smaller first spawning 1+ fish (Kim & Lo, 2001).

Other studies on many species of anchovy have suggested an association between the spawning fraction and female body mass, even in species found in different habitats (Claramunt *et al.* 2007). However spawning fraction has also been shown to increase with increase in temperature (Takasuka *et al.* 2005) with tropical species exhibiting

very high spawning fractions (Alheit, 1993). Motos (1996) reported spawning fractions of 0.18 at 15-18°C and 0.35 at 24°C for *E. encrasicolus*, reflecting similar results to those obtained in the current study. In South Australia the higher spawning fraction of smaller anchovies was also found in the warmer gulf waters. In addition to the influence of temperature, spawning fraction has also been found to be lower in populations in less stable variable habitats (Somarakis *et al.* 2005) which may also explain the lower spawning fraction of *E. australis* in offshore upwelling areas.

Although some studies on other anchovy species have reported sex ratios of 1:1 (Millan, 1999) most suggest female biased sex ratio (eg. Somarakis *et al.* 2004; Coterro-Altamirano & Green-Ruiz, 1997). In the current study, there was a higher percentage of females than males in both gulf and shelf regions. This greater abundance of females compared to males falls within ranges reported for other anchovy species and also suggests a higher female bias for smaller gulf fish than for the larger fish in the shelf waters. Higher female to male ratios at smaller sizes have also been reported for anchovy in *E. encrasicolus* (Shelton *et al.* 1993) as have higher ratios for inshore *E. mordax* in the Gulf of California over offshore fish in the California Current (Coterro-Altamirano & Green-Ruiz 1997).

Egg production estimates of 218 and 198 eggs m⁻², for gulf and offshore anchovies respectively, fell within published ranges for anchovies from the more oligotrophic regions inhabited by the European anchovy and those from highly productive upwelling areas. Egg production estimates ranged from 61 to 110 eggs m⁻² for *E. encrasicolus* in Europe (Melia *et al.* 2002; Somarakis *et al.* 2005) and up to 487 eggs m⁻² for *E. encrasicolus* in productive waters off South Africa (Shelton *et al.* 1993). Cubillos *et al.* (2007) reported 124 eggs m⁻² for *E. ringens* in southern Chile and values up to 474 eggs m⁻² have been reported for that species further north in more productive Peruvian waters. Values for *E. mordax* off California have ranged from 190 inshore and 230 offshore (Hewitt & Brewer, 1983). The position of *E. australis* within this range supports previous suggestions that this region's productivity lies at the lower end of the ranges of upwelling systems off California, Peru and South Africa (Ward *et al.* 2006).

The biomass estimates of over 101 000 and over 25 000 tonnes for shelf and gulf regions respectively indicate that, in spite of higher fish biomass per unit sea surface area in the gulfs, there is much less overall biomass in the gulfs, approximately a quarter of that occurring in shelf waters. This is not surprising given the much smaller area available. However anchovies in the gulfs are not less abundant than those occurring in offshore areas with approximately 6 billion anchovies responsible for the observed egg densities in the gulfs and similar number of anchovies occurring offshore, if average weights are used to derive rough estimates of absolute abundances from the biomass results for each region. While the offshore component is comprised of multiple age classes (including unknown numbers of young fish) the inshore fish all seem to be less than 1 year old (Dimmlich & Ward, 2006).

The estimates obtained in this study indicate that anchovy biomass dominates the inshore gulf regions, where sardines are absent, and that the offshore biomass may equal or indeed exceed that of sardine in shelf waters in some years (Ward *et al.* 2001b). Contemporary regional studies support our high estimates of anchovy abundance in South Australian waters. Anchovies appear to be highly important components of the South Australian marine ecosystem. They have been found in 80-100% of stomach samples from little penguins (*Eudyptula minor*) sampled in SA waters (Ward *et al.* 2008). In addition, anchovy may comprise almost a quarter (36.3%) of the diet of crested tern chicks, more than any other prey species (McLeay *et al.* 2009). Anchovies are likely to be a major component of the diet of many other bird, mammal and fish species in the region. Consequently, possible interannual fluctuations in anchovy biomass may be large enough to affect the structure and function of the pelagic ecosystems given the apparently high levels of consumption by predators, and the relatively high lipid content of anchovies compared to alternative prey species (Wiebkin, unpub. data).

According to the 'basin hypothesis' clupeoid population components exploit optimal areas or 'basins' for reproduction and, during periods of low abundance, the distribution of stocks shrinks with spawning essentially restricted to the more favourable spawning sites (MacCall, 1990). In years of low anchovy abundance in shelf

waters of South Australia it appears that the anchovy population is reduced to a much narrower demographic comprising largely young fish. While decreases in numbers of older, highly fecund, spawning age classes will decrease effective population fecundity (Smith *et al.* 1989) in the longer term, the large biomass of young fish found in this study provides a springboard for the rapid expansion of the population when conditions are favourable in offshore areas. Such a large reserve of young fish in these relatively stable environments may increase the resilience of anchovy in South Australia to unfavourable inter-annual changes in offshore environmental conditions, providing them an advantage over species restricted to an offshore distribution. Similar observations have been reported for *Engraulis japonicus* which are mainly found restricted to inshore waters when stock size is small but becomes more widely distributed as stock size increases, with more fish moving further offshore to spawn (Takasuka *et al.* 2005).

Size related separation of components of an *E. ringens* population have also been observed off central southern Chile which also resulted in stratification of the DEPM methodology (Cubillos *et al.* 2007). Although these fish were not aged, it is likely that population also is strongly partitioned by age as the published length frequency figures are almost identical to those reported in South Australia (Dimmlich & Ward, 2006). In such studies, the ages of population components should be considered as several DEPM parameters can be age dependent (Parrish *et al.* 1996) with significant impacts on both parameter accuracy and population reproductive potential (Somarakis *et al.* 2004).

The present study has extended our knowledge specifically of the ecology of anchovy in southern Australia and the adaptive potential of spawning engraulids in general. We have confirmed the results and support those of other investigations suggesting that variability in habitat conditions may directly influence anchovy reproduction (Kim & Lo, 2001; Somarakis *et al.* 2004). However, while the biomass estimate for anchovy in shelf waters may be considered as robust as those obtained in other DEPM studies on anchovy species elsewhere, the estimate of the biomass of gulf fish is more uncertain due to limitations of sample sizes in that region. A particular drawback in the present study is the lack of information on egg development rates at the high temperatures in

the northern gulfs. Further information is required to establish egg development keys which cover the range of temperatures recorded over the South Australian anchovy spawning areas. An examination of the variability in duration of postovulatory follicle stages over this temperature range may be informative.

In conclusion, this study suggests that biomass estimates of anchovy using the DEPM would be improved by a better understanding of spatial variations in the spawning patterns of fish at different ages and lengths. The DEPM can be quite insensitive to inadequate adult sampling if there are no substantial differences in spawning frequency among different groups (Somarakis *et al.* 2004). However, the results of our study support the conclusions of other recent studies which recommend that further investigation is needed to determine the relationship of spawning frequency to size/age and environmental factors (Claramunt *et al.* 2007).

Chapter 5

GENERAL DISCUSSION

In this thesis I present information on the anchovy, *E. australis*, for both the inshore and continental shelf waters of South Australia. Chapter Two provides the first comprehensive data on the geographic range of this species in South Australia in addition to the timing and locations of spawning. Although eggs and larvae were collected throughout shelf and gulf waters, the northern gulfs were notable for having significantly higher densities of eggs. However this higher egg density did not result in the highest larval survival rates which were recorded offshore near the regions of cool water up-welling over the shelf near western Eyre Peninsula and the western tip of Kangaroo Island.

The peak spawning period of January to March in South Australia determined by this study reflects spawning seasons of engraulids in other ecosystems which coincide with such up-welling events (Chesney and Alonso-Noval, 1989; Castro *et al.* 2000; Hernandez-Vazquez, 1994; Shelton and Hutchings, 1981; Roy *et al.* 1989; Beckley and Hewitson, 1994; Lafuente *et al.* 2002). This period also coincides with the peak spawning season of sardine in South Australia (Ward *et al.* 1998) and suggests the relationship between anchovy and sardine in this region which is further investigated in this thesis. These two species display broad scale overlap in spawning distributions in South Australia. Fluctuations in the relative abundance of *Engraulis spp.* and *S. sagax* in eastern boundary current systems have been attributed to changes in oceanic currents which favour one species over the other (Takahashi *et al.* 2009; Kawasaki and Omori, 1988) together with variations in up-welling intensity (Van Der Lingen, 2002) and wind stress curl (Rykaczewski and Checkley, 2008) that affect the availability of preferred prey items of each species. In southern Australia, significant (>70%) reductions in the abundance of adult *S. sagax* from mass mortality events in 1995 and 1998 (Ward *et al.* 2001) appeared to associate with, and perhaps relate to, concomitant increases in the spawning area and total abundance of anchovy eggs and larvae (Ward *et al.* 2001). This

is similar to other studies which indicate anchovies increase when and where sardines are either absent or at a low population density (Rodriguez-Sanchez *et al.* 2002).

Typically the trigger for a change in the population density between these two species is a formation of one or more strong year classes as a result of a convergence of environmental conditions favouring spawning and higher survival rate in one of the species (Nakata *et al.* 2000). However, in South Australia an unusual, and seemingly temporary, regime shift appears to have been triggered by external factors that decimated parts of the sardine population. Prior to the expansion in anchovy spawning activity following the high mortality events of the sardine, anchovy spawning was generally confined to Spencer Gulf and Gulf St Vincent. Anchovy eggs have been shown to be a major component of sardine diet (Alheit 1987; Valdes-Szeinfeld 1991; Van der Lingen 2002). The reduction, by over 70%, of the sardine population may have reduced the predation pressure on anchovy eggs in shelf waters and thus facilitated high survival rate and hence an expansion of anchovy spawning habitat beyond gulf waters (Ward *et al.* 2001). This unusual event, whilst not strictly analogous to normal regime shifts observed for other anchovy/sardine ecosystems, has provided a unique opportunity to investigate the response of an anchovy population to a drastic reduction in the local sardine population.

However, success by anchovies in open ocean regions may be considered anomalous with few examples of offshore ecosystems dominated consistently over a long period by anchovies. The long-term success of anchovies off Peru, for example, has been attributed to conditions peculiar to that low latitude location which, because of a weakened coriolus effect, presents a relatively benign habitat in terms of offshore transport and particle residence times (Bakun and Weeks, 2008). More frequently the offshore habitats, such as the northern Benguela off southern Africa and Kuroshio off Japan, are characterised by dominant sardine stocks (Barange *et al.* 2009) over the long term. Skud (1982) identified general patterns in a number of fishes that seem to form interrelated 'pairs' (as often exhibited by anchovies and sardines) such that the population dynamics of the dominant species tends to respond to environmental factors while those of the subordinate species responds to the abundance of the dominant one.

Any long-term patterns of sardine-anchovy interaction/alternation in the South Australian region have not been documented due to the limited time series of available data. However, it may be possible to suggest, from the recent rapid recovery of the sardine population in a region dominated by anchovy, that the South Australian shelf area is a 'natural' sardine system, where anchovies are the subordinate species. Examples of anchovy intermittently replacing sardine have been recorded elsewhere, including the Gulf of California (Bakun *et al.* 2010).

The current survey established that the gulf habitats were characterised by relatively high water temperatures, approaching 26° C during the summer spawning season of the anchovy (Chapter Two; Dimmlich *et al.* 2004) and appeared to support higher than average spawning densities of anchovy in Australian waters. However numbers of larvae declined rapidly with increase in age and few larger larvae were recorded in the sampled areas. It should be noted that absence of large (> 10 mm) postflexion larvae in the samples does not imply absence from the area, merely that they are better able to evade the sampling gear at that size. Although it is possible that emigration to nearby habitats could account for the decrease in abundance there was no evidence to show this. In contrast, lower egg densities and higher larval densities were found to occur in offshore areas near the up-welling regions. This suggests that survivability of larvae was higher in the offshore regions and therefore the most favourable nursery areas for the anchovy is likely to be the region where greater abundances of larger larvae, rather than high egg densities, were found to occur. This result is in agreement with studies (Peterman *et al.* 1988; Cole and McGlade, 1998) which have proposed that levels of recruitment to the juvenile stage may be correlated with survival rates of larvae > 10 mm and with the strength of up-welling processes where productivity is enhanced.

Although significant anchovy spawning activities were reported in Chapter Two, information was not available for the age-structure of the populations responsible for the high densities of eggs recorded in gulf and shelf waters. However, it appeared that one component of the population was spawning in the closed circulation system of the northern gulfs and another component was spawning in the more dissipated habitat associated with the offshore up-welling regions. Chapter Three presents the

investigations into the age-structure of the South Australian anchovy population.

Ageing of fish captured during field-sampling using both length- and otolith-based methods suggested that anchovies in South Australia reached a maximum age of five years; an age comparable to that of other longer lived anchovy species (Spratt, 1975; Bellido *et al.* 2000). These five year old fish were found exclusively in offshore shelf waters and, generally, all offshore fish were predominantly greater than 3 years old. The upwelling conditions in these waters appear to be favourable for anchovy spawning (Chapter Two; Dimmlich *et al.* 2004), presumably because the high concentrations of planktonic food required by first feeding anchovy larvae can be found in the upper water column (Blaxter and Hunter 1982).

The youngest fish were found exclusively in northern gulf waters where they attained a maximum age of approximately one year. A third grouping of fish was concentrated near the southern gulf where gulf waters are separated from the up-welling zones by temperature and salinity frontal systems (Bruce and Short, 1992). This group was comprised of a mix of ages but did not include either the youngest fish (found only in the northern gulfs) or the oldest fish (which were found only in shelf waters). These results thus strongly suggest that the anchovy exhibits size and age-related distribution patterns in South Australian waters and were consistent with observations for other engraulid species, such as *E. mordax* (Curtis 2004) and *E. encrasicolus* (Barange *et al.* 1999), which tend to move further offshore as they age. It is important to note that inshore areas of the extensive South Australian coastline were not able to be sampled and that it is likely that another component of the anchovy population is also present in those areas. The age structure of these coastal inshore fish is not known but it is likely that additional spawning and nursery areas would be located in the larger embayments.

To summarise, there appears to be evidence that there are three identifiable components to the anchovy population. The young fish, to one year of age, occurring in the enclosed gulf areas, 2-3 year old fish at the mouths of the gulfs and older fish over the shelf. This age gradient is expected to be mirrored in other embayments and inshore areas of South Australia but is likely to be far less well defined over a much reduced

spatial scale, ie. 10's of kilometres, rather than 100's of kilometres.

There was no evidence of movement by older fish back to the northern gulf areas. This is contrary to a postulated 'duo phase' anchovy life cycle (Blackburn 1950) in which older fish return to inshore spawning areas waters in later years. The difference between these studies may be due to the different ageing methods used. Blackburn (1950) utilised scale-based methods which have been shown to underestimate growth rates, resulting in that study identifying fish at 60 mm as one year old. Using both scale-based and length-based methods in the present study, the estimated length of local anchovy at one year in South Australia was larger, at approximately 110 mm. Blackburn (1950) may have attributed fish at this size to an older cohort of two year old fish and this could, perhaps, have suggested the existence of a 'duo phase' life cycle.

Such strong age/size partitioning of components of an anchovy population have been observed elsewhere. Recently, size partitioning within the *E. ringens* population off central southern Chile resulted in the stratification of the stock assessment methodology used to assess the biomass of anchovy in the region (Cubillos *et al.* 2007). Assessment of the total biomass in South Australia (Chapter Four; Dimmlich *et al.* 2009) similarly required independent estimates of key parameters used in the daily egg production methodology (DEPM). Several DEPM parameters can be age dependent (Parrish *et al.* 1996) including average female weights, batch fecundity and spawning fraction. Attempts to estimate these parameters for the entire population would produce inaccurate results for each component. The current study represents the first investigation of variations in these parameters within the context of a single anchovy population displaying distinct age- and region-specific differences.

The difference in estimates of mean batch fecundities between the shelf and gulf of 15,572 and 855 eggs respectively highlights the need to stratify the methodology. The high fecundities of the larger offshore fish were typical of other *Engraulis* species at similar sizes. However, apart from *E. japonicus* in Korean waters with mean batch fecundities of between 485 and 1003 (Kim & Lo, 2001), there are few other studies on anchovies of similar body mass. The large difference in fecundity between the gulf and

shelf anchovies is directly related to the size difference in spawning females in the two regions. Anchovies in South Australia attained their maximum adult growth rates between the first and second years (Chapter Three; Dimmlich *et al.* 2006) and, by their second spawning season, had almost attained a maximum size with commensurately larger ovaries producing a higher number of eggs .

Although the smaller fish had lower batch fecundities, the estimates of spawning fraction of 0.16 and 0.34 for shelf and gulf anchovies respectively, indicated that female anchovies in the gulfs were spawning more than twice as frequently as the larger fish. There was approximately one week between spawning events for shelf fish and a far lower interval of approximately three days for the smaller gulf fish. Similar ratios have been reported for other *Engraulis* species (Cubillos *et al.* 2007; Kim & Lo, 2001) with spawning fraction seeming to be strongly dependent on female body size (Claramunt *et al.* 2007).

One of the factors contributing to the higher spawning fractions in the one year old adults may be the relatively high water temperatures recorded in the gulf waters (Chapter Two; Dimmlich *et al.* 2004). The spawning fractions of anchovy species have been shown to be positively correlated with ambient water temperature (Takasuka *et al.* 2005) with tropical species exhibiting very high spawning fractions (Alheit, 1993) and spawning fractions of 0.18 at 15-18°C and 0.35 at 24°C for *E. encrasicolus* (Motos 1996) reflecting similar results to those obtained in the current study. In addition to the influence of temperature, spawning fraction has also been found to be lower in populations in less stable variable habitats (Somarakis *et al.* 2005) which may partly explain the lower spawning fraction of *E. australis* in offshore up-welling areas of South Australia.

Despite the differences in fecundity and spawning fraction, egg production for the two regions was similar. This resulted in a relatively high biomass estimate for the northern gulfs, considering the much smaller area available for spawning compared to the expansive shelf waters. The egg production estimates of 218 and 198 eggs m² for gulf and shelf anchovies respectively fall within the range of 61 to 487 eggs m² defined by

anchovy egg production within the more oligotrophic regions inhabited by the European anchovy and those from highly productive up-welling areas (Melia *et al.* 2002; Somarakis *et al.* 2005; Shelton *et al.* 1993).

Despite the higher biomass ratio of shelf anchovies (101, 000 tonnes) to gulf anchovies (25, 000 tonnes), the estimates of absolute abundance, ie. numbers of individual fish, were similar for the two regions. However the gulf population is comprised solely of fish less than one year of age whereas the offshore population comprises multiple year classes. During years when the population over the shelf is reduced, whether through competition with sardines or by abiotic/oceanographic factors, it may be reduced to a much narrower demographic in inshore and gulf waters. This inshore population, inhabiting relatively stable environments where anchovy are the dominant species, may form a large reserve of young fish from which the population may expand when offshore conditions become more favourable. Similar suggestions have been made with regard to *Engraulis japonicus* which are mainly found restricted to inshore waters when stock size is small but become more widely distributed as stock size increases, with more fish moving further offshore to spawn (Takasuka *et al.* 2005).

CONCLUSIONS

The anchovy population in South Australia appears to be relatively small in comparison to anchovy populations in very productive upwelling zones such as the California, Humboldt and Benguela systems. The levels of egg production by *E. australis* within this region supports suggestions that this region's productivity lies at the lower end of the ranges of upwelling systems off California, Peru and South Africa (Ward *et al.* 2006). However, recent research has suggested that the upwelling has enhanced the productivity in this region such that it may approach that of the productive eastern boundary current systems (Van Ruth *et al.* in press). The lower anchovy egg production results observed in this study may therefore be influenced by factors other than regional productivity.

Recent studies have begun to investigate the range of adaptive strategies which anchovies have evolved throughout these various boundary current systems (Bertrand

et al. 2005). This study suggests that anchovy in South Australia, through their broad tolerance range of conditions, are able to exploit widely differing environments during the summer-autumn spawning season.

The results of this study suggest that, of the two forage fish species dominating the South Australian marine ecosystem, only anchovies can exploit the relatively benign environment found in the warm and saline waters of the northern Spencer Gulf, where an almost closed circulation system exists (Bullock 1975). In this large area of the gulf (approximately 500 km²) the retention of larvae is maximised and the habitat is generally homogeneous during the extended spawning season providing a consistently favourable nursery for *E. australis*. Other small pelagic species in the up-welling system of southern Australia spawn under more unpredictable environmental conditions of the shelf. The apparent increase in the distribution and abundance of anchovy resulting from two mass mortalities of sardine (Ward *et al.* 2001a), in conjunction with results from the present study, suggests that sardine abundance may affect the survival rates of anchovy larvae in shelf waters of South Australia. It is possible that anchovy larvae may effectively utilise the up-welling zones outside the gulfs when levels of sardine abundance in shelf waters are low. The warm northern and mid-gulf waters, while not the ideal spawning or nursery environment, lie outside the range of temperatures tolerated by sardines (Van der Lingen, 2001, Ward *et al.* 2003) and may be critical for sustaining the South Australian anchovy population during periods when sardine abundance is high. Additionally, anchovies throughout the world exhibit a generally higher degree of affinity for inshore and/or estuarine-affected habitats than do sardines, perhaps due to their much coarser gillraker structures (Bakun *et al.* 2010). While not capable of filtering food particles as small as can sardines, anchovies may be less likely to experience clogging of these structures as a result of higher sediment loads and other matter which may characterise inshore areas

This study has greatly extended our understanding of the ecology of *E. australis* in southern Australia and the adaptive potential of spawning engraulids in general. The results support those of other investigations suggesting that variability in habitat conditions may directly influence anchovy reproduction (Kim & Lo, 2001; Somarakis *et*

al. 2004).

Finally, the estimates of population size of *E. australis* in South Australia enable a positioning of the local anchovy stocks within a global perspective and an evaluation of the potential for a local fishery. As the potential for a local fishery is realised the ecological and biological information and estimates of population size obtained by this study may facilitate appropriate management of anchovy stocks in South Australia so that populations are maintained into the long term future.

FUTURE RESEARCH

A particular limitation in the present study, which has implications for future application of the DEPM in the management of anchovy stocks in South Australia, is the lack of information on egg development rates at the high temperatures in the northern gulfs. Further information is required to establish egg development keys which cover the range of temperatures recorded over the South Australian anchovy spawning areas. Additionally an examination of the variability in duration of post-ovulatory follicle stages over this temperature range is also required for future population estimates. Further investigation is also desirable to further determine the relationship of spawning frequency to size/age and environmental factors, a recommendation which has also been made following the application of the DEPM to other anchovy species where different size and age defined components spawn in spatially distinct areas (Claramunt *et al.* 2007).

The results of this study suggest that similar strategies of spawning by one year old fish in sheltered inshore waters, prior to a move further offshore by older fish in subsequent spawning seasons may be occurring in other Australian waters where age gradients have been found to occur (Blackburn 1950; Hobday 1992; Hoedt *et al.* 1995). However to confirm this, more comprehensive ageing of anchovies in these locations is required as the results of scale-based studies (Blackburn 1950) in these regions appear to differ significantly from the results of the present study. Further investigations into the apparent movement from gulf to shelf waters by anchovy may benefit from the use of

otolith microchemistry methods.

Finally, continuing investigation of the relationship between the sardines and anchovies in South Australia may provide further information on differential space occupation patterns during population growth and decline. While it appears that anchovy may require suitable habitat to become available for the population to grow, habitat availability may not be a pre-requisite for sardine population expansion and growth (Barange *et al.* 2009). Recent studies suggest that additional factors, such as plankton size and abundance, related to variations in rates of wind-forced upwelling, may also have a significant impact on sardine and anchovy abundance (Rykaczewski and Checkley, 2008). It is likely that the natural ecological mechanisms which may potentially permit the expansion of anchovy over shelf areas are more complex than a simple replacement caused by the removal, due to probable anthropomorphic causes (Ward *et al.* 2001), of sardines from the South Australian marine ecosystem. The rapid recovery of the sardine population following the equally rapid expansion of anchovy throughout shelf waters recorded and described in this study suggests that the dominant 'wasp-waist' role in the South Australian shelf ecosystem belongs to the sardine.

Appendix A – Title Page Reprints.

FISHERIES OCEANOGRAPHY

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Relative importance of gulf and shelf waters for spawning and recruitment of Australian anchovy, *Engraulis australis*, in South Australia

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ABSTRACT

Gonosomatic indices and egg and larval densities observed from 1986 to 2001 suggest that the peak spawning season of the Australian anchovy (*Engraulis australis*) in South Australia occurs during January to March (summer and autumn). This coincides with the spawning season of sardine (*Sardinops sagax*) and the period when productivity in shelf waters is enhanced by upwelling. Anchovy eggs were abundant throughout gulf and shelf waters, but the highest densities occurred in the northern parts of Spencer Gulf and Gulf St Vincent where sea surface temperatures (SST) were 24–26°C. In contrast, larvae >10 mm total length (TL) were found mainly in shelf waters near upwelling zones where SSTs were relatively low (<20°C) and levels of chlorophyll *a* (chl *a*) relatively high. Larvae >15 mm TL were collected only from shelf waters near upwelling zones. The high levels of larval abundance in the upwelling zones may reflect higher levels of recruitment to later stages in these areas compared with the gulfs. The sardine spawns mainly in shelf waters; few eggs and no larvae were collected from the northern gulfs. The abundance of anchovy eggs and larvae in shelf waters increased when sardine abundance was reduced by large-scale mortality events, and decreased as the sardine numbers subsequently recovered. We hypothesize that the upwelling zones provide optimal conditions for the

survival of larval anchovy in South Australia, but that anchovy can only utilize these zones effectively when the sardine population is low. At other times, northern gulf waters of South Australia may provide a refuge for the anchovy that the sardine cannot utilize.

Key words: anchovy (*Engraulis australis*), clupeoid, eggs, inshore–offshore distribution, larvae, sardine (*Sardinops sagax*), spawning, upwelling

INTRODUCTION

Anchovies (*Engraulis* spp.) inhabit inshore and continental shelf waters of temperate and subtropical regions. Their spawning patterns vary in response to a range of environmental factors (Castillo *et al.*, 1996; Castro *et al.*, 2000; Kim and Lo, 2001; Ward *et al.*, 2003) with the peak spawning period often occurring during warmer months and/or periods when productivity is enhanced by seasonal oceanographic processes (Roy *et al.*, 1989; Nelson *et al.*, 1994; Borja *et al.*, 1998; Aoki and Miyashita, 2000). Spawning usually occurs throughout coastal and shelf waters (Brewer and Smith, 1982; Fletcher and Tregonning, 1992; Beckley and Hewitson, 1994; Hoedt and Dimmlich, 1995); however, the relative importance of inshore/offshore waters for spawning and the survival of eggs and larvae is poorly understood.

Significant differences in the levels of anchovy spawning activity in inshore and offshore waters have not been identified, but some studies have suggested that rates of larval survival are higher in some inshore areas (Brewer and Smith, 1982; Hewitt and Brewer, 1983; Castro *et al.*, 2000). In the eastern and western boundary current systems, the key spawning areas usually coincide with the main larval nursery areas (Hernandez-Vazquez, 1994; Smith *et al.*, 2001). Where key spawning and nursery areas are spatially decoupled, the optimum spawning grounds are frequently located relatively close to the main nursery areas or utilize prevailing currents to facilitate movement of eggs/larvae from the spawning grounds to the

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Spawning dynamics and biomass estimates of an anchovy *Engraulis australis* population in contrasting gulf and shelf environments

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The spawning biomass of Australian anchovy *Engraulis australis* in gulf and shelf waters of South Australia was compared using the daily egg production method (DEPM). The total survey area was 128 700 km² with recorded spawning areas in gulf and shelf waters of 4898 and 44 618 km², respectively. High egg densities in the warm, shallow gulf waters were produced by small, young (<1 year old) *E. australis* that spawned relatively small batches of eggs (c. 855) approximately every 3 days. In cooler, deeper shelf waters, where larger, older *E. australis* are found, lower egg densities occurred despite individuals producing much larger batches of eggs (c. 15 572) approximately every 7 days. In shelf waters, the highest densities were recorded at inshore sampling stations. Spawning appeared to peak between 0000 and 0100 hours. Females were more abundant than males in samples from both gulf and shelf waters with sex ratios of 0.61 and 0.56, respectively. The spawning biomass of *E. australis* in shelf waters was 101 522 t, whereas the estimate for gulf waters was 25 374 t. Due to the differences in mean size of the spawning females, however, c. 6×10^9 *E. australis* were present in each region. The results support the hypothesis that variability in habitat conditions may directly influence *E. australis* reproduction. A large reserve of young fish in the relatively stable gulf environment may increase the resilience of the *E. australis* population in South Australia to unfavourable interannual changes in offshore environmental conditions.

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Key words: Clupeidae; daily egg production; fecundity; reproduction; South Australia; stock assessment.

INTRODUCTION

Clupeiformes are able to utilize a range of flexible behaviours to maximize recruitment in the dynamic pelagic environments typical of productive coastal upwelling zones (Bertrand *et al.*, 2004; Robinson, 2004). These key prey species usually comprise a high proportion of the total biomass in such ecosystems (Schwartzlose *et al.*,

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